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TREE-BASED BUFFER SYSTEMS: THEIR IMPORTANCE AT THE LANDSCAPE LEVEL UNDER SHIFTING CLIMATE SCENARIOS

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SIMULATING THE IMPACT OF HUMAN LAND USE CHANGE ON FOREST COMPETITION IN GREAT PLAINS AGROECOSYSTEMS WITH THE *SEEDSCAPE* MODEL

by

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ABSTRACT.

The expansion and contraction of marginal cropland in the Great Plains often involves small forested strips of land that provide important ecological benefits. The effect of human disturbance on these forests is not well known. Because of their unique structure such forests are not well-represented by forest gap models. In this paper, the development, testing and application of a new model known as ***Seedscape*** is described. ***Seedscape*** is a modification of the JABOWA-II model, and it uses a spatially-explicit landscape to resolve small-scale features of highly fragmented forests in the eastern Great Plains. It was tested and evaluated with observations from two sites, one in Nebraska and a second site in eastern Iowa. ***Seedscape*** realistically simulates succession at the Nebraska site, but less so at the Iowa site. ***Seedscape*** was then applied to the Nebraska site to simulate the effect that varying forest corridor widths--in response to the presumed expansion/contraction of adjacent agricultural land--has on succession properties. Results suggest that small differences in widths have negligible effects on forest composition, but large differences in widths may cause statistically-significant changes in the relative importance of some species. A testable hypothesis that a critical forest width must be achieved in order to affect processes of succession is suggested.

KEY WORDS: gap models, land use change, riparian forests, biodiversity, agroecosystems

1. INTRODUCTION

The U. S.Great Plains is predominantly an agricultural landscape in a semi-arid temperate grassland biome. The region produces about 25% of the nation's grain crops and nearly one-third of its livestock (USDA 1990). Cropped land accounts for 60 million hectares or 50% of the total land area of the region and approximately 33% of total U. S. cropland (USDA 1990). These numbers have been relatively stable for most of this century (Crosson, 1992). However, Bratton et al (1995) note conflicting forces over the management of marginal agricultural land maintained as shelterbelts and riparian forests. Such agricultural land provides important ecological benefits noted below. Historically, farming practices (especially the clearing of productive river bottoms and unrestricted livestock grazing) have led to large-scale elimination of riparian forests (Bratton et al 1995). Yet, several U. S. government programs provide incentives to farmers to expand farm woodlands (e.g., Forestry Incentives Program, Conservation Reserve Program, Stewardship Incentives Program). These conflicting forces keep the extent and quality of Great Plains forests in a constant state of flux.

In the future, rising world agricultural demand coupled with increasingly volatile crop prices are likely to pressure Great Plains farmers over the long run to increase their outputs in order to maintain or increase profitability (Crosson, 1989). Most of the increase will probably come from technical improvements that raise the productivity of land already in production, but, surely, some of the increase will come from the expansion of cropland. By extension, agricultural land held in shelterbelts and riparian forests could be diminished with unknown consequences for the ecological services they provide. The purpose of this paper is to simulate

the effect of changing widths of shelterbelts and riparian forests in the Great Plains on tree species composition using the newly developed ***Seedscape*** model.

In agroecosystems of the Great Plains, trees play important roles in crop production through their sheltering effects (Kort 1988), filtering agricultural contaminants from runoff (Lowrance et al. 1984, Peterjohn and Correll 1984), and provision of relatively undisturbed habitat for wildlife in cultivated areas (Schroeder 1986, Schroeder et al. 1992). As society increasingly values the services provided by trees in these agricultural landscapes, strong arguments can be made for a greater understanding of Great Plains forest ecology. We assert, however, that the growth and succession of forests in these regions have been largely overlooked.

Because forest succession takes a long time, modeling is a powerful tool to simulate the succession of forests. Among many forest models, gap models (e.g., Shugart 1984, Botkin 1993) have been especially well developed. In such models, the establishment, growth, reproduction, and death of individual trees on a small plot of land (commonly 10 x 10 m) are simulated, and the forest dynamics simulated on this plot are assumed to represent the surrounding forest.

Some assumptions that underlie gap models have been criticized, such as reliance on growth functions that are based on empirical estimates of responses to growing degree days rather than on physiological responses to temperature (e.g., Bonan and Sirois 1992). Nevertheless, gap models have been used successfully to simulate forest dynamics in forested regions throughout the world (Shugart 1984, Shugart et al. 1992). Most current gap models are derived directly or indirectly from the FORET model (Shugart and West 1977), which in turn was derived from the JABOWA model (Botkin et al. 1972).

Individual-based modeling is a reductionistic tool for simulating ecosystems (Liu and Ashton 1995, Grimm 1999, Lorek and Sonnenschein 1999). Individual-based forest gap models simulate the regeneration, mortality, and growth of forest trees based on the physiological responses of individual species (Botkin et al. 1972, Urban et al. 1993). They provide a powerful tool for describing the forest dynamics in heterogeneous environments because they are mechanistic, and arrays of these models can simulate different parts of the landscape (Pausas et al. 1997). In recent years, gap models have been extensively used and greatly improved (Malanson et al. 1992, Bugmann 1996). For example, Liu and Ashton (1998) developed a forest simulation model called FORMOSAIC which also considers the influences from neighboring areas in the landscape mosaic (see also Liu and Ashton, 1999). Despite considerable progress in forest growth modeling, the performance of gap models in regions where forests are a minor but ecologically important component of the landscape has not yet been adequately tested. Direct application of extant gap models to the fragmented, linear forests of the Great Plains is difficult because the models were originally designed for large contiguous forest tracts.

Patchy forests present several problems for gap models. Seeds disperse throughout the landscape, and this dispersal must be captured by the model if succession is to be represented accurately (Hanson et al. 1990). In most gap models, a single plot is assumed to represent a large area. Such models usually include ubiquitous seed dispersal, assuming that the plot will receive an unlimited number of seeds of all species that might occur in the landscape (see Liu and Ashton 1998). Establishment of trees in this scenario is entirely dependent on the survival of seedlings, rather than the arrival of their seeds in the plot. In reality, the location of any plot in the landscape will affect its probability of receiving seeds that disperse from other isolated plots

in the landscape (Liu and Ashton 1998). This is particularly true for highly fragmented forests such as those found in the agricultural landscapes found in the Great Plains. Therefore, a single plot cannot be assumed to represent the entire forest accurately.

The linear shape of many forest corridors is not represented well by gap models that assume a large contiguous forest. Linear forests result in a greater proportion of trees in the landscape that are on the forest's edge, where they are likely to experience greater light availability and a different microclimate than interior trees (e.g., Kupfer and Malanson 1993a). In addition, the Great Plains comprises a mixture of upland and riparian forests. These two forest types experience very different water regimes. The water table in upland areas is extremely deep in many parts of the Great Plains. Trees in upland areas of the Great Plains gain all of their water directly from precipitation. In riparian forests, however, water is also available from adjacent streams or rivers and the availability of this water may fluctuate with season and runoff from adjacent fields.

Guertin et al. (1997) established the conceptual basis for modeling forests in a landscape dominated by agriculture, laying the foundation for a new model known as ***Seedscape***. In the remainder of the paper, we describe ***Seedscape***, a modified gap model developed specifically for linear forests of Great Plains agroecosystems. Compared with many earlier gap models, this model can simulate multiple plots and allows seed dispersal throughout the simulated landscape, and it also distinguishes upland and riparian forests by varying water table characteristics between the two. We then test the model by comparing its simulations with observed data (some of which were used to construct the model). Finally, we apply the model to the question: how do

long-term changes in farming practices that modify the areal extent of such forests affect successional processes and resulting forest composition?

2. METHODS

2.1 The *Seedscape* model

The basic structure of ***Seedscape*** is derived from the existing gap model JABOWA-II (Botkin 1993). The JABOWA-II model deals with many species and uses physiological response to explain the growth of individual trees. The model was developed to successfully mimic the growth of a community of trees in a changing environment. In the model, a tree is described according to species, diameter and height. Environmental factors that affect tree growth include light, temperature, soil nitrogen, soil-water depletion, and soil-water saturation.

The model was expanded to allow simulations over many plots in a spatially explicit landscape. This enables the incorporation of fundamental differences between forest stands with small edge-to-area ratios (e.g., large forested tracts) and ones with large edge-to-area ratios (e.g., riparian forests).

2.1.1 Spatially explicit landscape

The most fundamental change to JABOWA-II is the replacement of a single 10 x 10 m plot with a grid of 10 x 10m plots. For example, a 1 km^2 landscape can be represented by 10,000 10 x 10m plots in a 100 x 100 grid. Within this landscape, each plot is assigned particular values for soil type, initial vegetation, and whether the plot is in a riparian or upland location. The soil type determines moisture capacity, available nitrogen in the soil, soil depth and the depth to the water table. In riparian locations, the depth to the water table is shallower and is allowed to

fluctuate. Initial vegetation determines whether the plot is cultivated, therefore incapable of supporting trees, or wooded. The species and diameter of all trees on each wooded plot are assigned at the start of the model run. In addition, because the 1 km^2 landscape is not a closed system, plots along the edges of the landscape can be designated as seed sources. These plots contain species that are found outside the 1 km^2 landscape, but are close enough to deliver seeds to the landscape.

2.1.2 Seed dispersal throughout a landscape

An essential feature of multi-plot gap models is the representation of seed dispersal among all of the wooded plots in the landscape (Hanson et al. 1990). ***Seedscape*** uses the dispersal algorithm from the SEEDFLO model (Hanson et al. 1990). This algorithm specifies each plot as a potential seed source, provided two conditions are met: 1) the plot contains trees large enough to produce seed (initially each tree's age is set to the minimum age for seed production unless explicitly set to another age); and 2) those trees actually produce seeds in a given year, as determined by the species-specific probability of seed production (Table 1).

For each tree on each plot, the probability of seeds reaching each of the other potentially wooded plots in the landscape is determined by the simple distance-decay function (see Okubo and Levin 1989):

$$P_{ij}=d_j^{-\phi_i} \qquad (1)$$

where i is a species-specific dispersal agent, P_{ij} is the probability of a seed dispersing to plot j given a dispersal agent i (Table 1), d_j is the distance in meters to plot j, and ϕ_i is the dispersal parameter for a dispersal agent *i* (see also Malanson and Armstrong 1996) (Table 2). This is a

simple, yet widely used, method of modeling seed dispersal. It does, however, ignore moving water and birds as dispersal mechanisms.

2.1.3 Growth, Establishment, and Death

Once seeds have arrived on a plot, the simulation of seedling establishment, growth, and mortality are similar to other existing gap models. The specific equations in ***Seedscape*** are the same as those in JABOWA-II (Botkin 1993). Growth parameters describe the maximum potential growth rate for each species, which is limited by environmental conditions such as the availability of light, nitrogen, water and temperature. If a tree does not grow during the growing season, the model considers the tree to be dead and removes it from the plot.

2.1.4 *Availability of water*

The availability of water depends on whether the plot is considered riparian or upland. For upland plots, the availability of water is the same as in JABOWA-II, and is determined by precipitation events and by the water table. Because the water table in our study areas is extremely deep in upland locations, it is not normally a factor in tree growth.

In riparian plots, however, the soil may be completely saturated due to a shallow local water table resulting from flooding along watercourses following precipitation events. ***Seedscape*** therefore allows for variable local water tables in riparian plots. The water table varies with water volume in the streams, which is in turn a function of runoff from surrounding agricultural fields. ***Seedscape*** uses the SCS (now NRCS) curve number method (USDA, Soil Conservation Service, 1972) to calculate runoff volume following precipitation events.

2.2 Data and Modeling Procedures

Modification of JABOWA-II to produce ***Seedscape*** was accomplished with data from a site in eastern Nebraska. ***Seedscape*** was tested with data from the Nebraska site and from an additional site in eastern Iowa.

2.2.1 *Nebraska*

Seedscape was initially developed for a small riparian corridor about 20 m wide located at the University of Nebraska Agricultural Research and Development Center, Saunders County, Nebraska. The study corridor is typical of those found in the eastern and central Great Plains. It is along a drainage slough with a total length of approximately 4 km. A 1.4 km section of this slough was cleared in 1979 and the 1 km square landscape used in this study was along this section of the corridor. Most of the landscape is agricultural with small plantings of trees interspersed. Areas surrounding this landscape have plantings of shelterbelts and more extensive stands of native trees along a larger riparian zone. Field data were gathered on existing vegetation in 1995 from five 10 x 10 m plots along the study corridor. The number of stems of each tree species and diameter of all trees were recorded, and a visual survey was made of the surrounding area to estimate the number and diameter of the potential seed source trees. Twelve species were in the 1 km^2 landscape including the seed source plots and 10 of these species were found in the riparian strip. The riparian corridor was initialized to have no woody vegetation at the start of the simulations.

Monthly weather data were obtained for 1967-1995 from the nearest weather station located at Mead, Nebraska. Soil types were determined from county soil survey maps. Since forests in the Great Plains are only 20-100 years old, our simulations are shorter in terms of number of years run for the model compared with other published models, e.g., SEEDFLO

(Hanson et al. 1990) and JABOWA II (Botkin 1993). Two iterations of a 100-year simulation for each of three different corridor widths (10, 20 and 100m) were simulated to diminish the effect of random number selection.

2.2.2 *Iowa*

A second site was located in the Red Cedar Wildlife Area (RCWA) on the west side of the Cedar River (cutbank edge), Muscatine County, Iowa (Kupfer and Malanson 1993a,b). The cutbank edge-effect is similar to the agricultural field edge-effect at the Nebraska site. The RCWA site is typical of riparian forests at the eastern edge of the Great Plains and the western edge of the rainfed Corn Belt.

The RCWA contains roughly 1.5 km^2 of continuous forest, which is distinctly different from the Nebraska site. Kupfer and Malanson (1993a) indicate that cutback erosion along the Cedar River has occurred at a mean rate of approximately 100 meters per century. Ten 16 x 16 m plots were surveyed by Kupfer and Malanson in each of the forest interior and the cutbank edge locations. The number of stems of each tree species and diameter of all trees were recorded. Twenty-three species were identified at both the cutbank edge and forest interior. Twenty-two of these species were found at the cutbank edge and 16 species in the forest interior. All of the species that were in the forest interior occurred in the cutbank edge except *Ostrya virginiana.* Seven species that occurred on the cutbank edge did not occur in the forest interior. These field data show a distinction between the cutbank edges and forest interior.

Monthly weather data were obtained for 1948-1995 from the nearest weather station at Muscatine, Iowa. Soil types were determined from Muscatine County soil survey maps. The model ran for two iterations of a 100-year simulation to diminish the effect of random number

selection. The cutbank edge plots were identical to the forest interior plots at the start of the simulations. Because the Iowa landscape was mostly forested, the seed-dispersal algorithm was time consuming in calculating seed-dispersal probabilities among all pairs of plots in a 10,000 plot landscape. The size of the landscape was therefore reduced to 0.9 x 0.9 km to decrease the model run time.

2.2.3 *Testing the model*

Data from the Nebraska and Iowa sites measure recent conditions only--i.e., no time series were available to compare with dynamical model simulations. Hence, our tests hinge on assumptions of initial forest state (known for Nebraska and estimated for Iowa) and the succession time required to move from that initial state to the current observed state (known for Nebraska and estimated for Iowa).

Model results were compared with existing vegetation using relative dominance, relative density and relative importance values for each species simulated in the model and observed on the surveyed plots. Relative dominance is the percent of the basal area for a species divided by the total basal area (values from 0-100% for each species). Relative density is the percent of the number of trees for a species divided by the total number of trees (values from 0-100% for each species). Relative importance is calculated as the sum of relative density and relative dominance (values from 0-200% for each species).

The relative (dominance, density and importance) value from each of the survey plots (five for Nebraska and 10 for Iowa) was subtracted from the averages of the relative values for the model plots (396 for Nebraska and 174 for Iowa) to take into account the unequal sample size between the model and surveyed plots, and the variation between the surveyed plots. None of

the survey plots in Nebraska contained all 10 species and none of the surveyed plots in Iowa contained all 22 species. A multiple t-test was used to determine the significance of differences between the model results and survey data. For Nebraska, vegetation in the surveyed plots along the riparian corridor were compared with the average model output from the 20m width at 20 years. For Iowa, vegetation in the surveyed plots along the cutbank edge was compared with averaged model output at 100 years. After 100 years, erosion along the Cedar River exposes the model's initial interior plots at the cutbank edge.

2.3 Simulation and Analysis Methods

Seedscape was executed within a Unix operating system. ***Seedscape*** programming is coded in C++ language and can be executed under many different platforms. It models tree growth on a yearly time step. Two replicates or iterations were performed. The two replicates were performed to damp the effect of random number selection at the beginning of the model run. Model data were output every five years. Model output includes the number and diameters of trees.

A realistic application of ***Seedscape*** is to examine the effect of varying forest corridor widths--in response to varying levels of forest/cropland conversion--on simulated relative importance values for a selection of species. We discussed the basis for this examination in the introductory section above.

Eleven of the twelve species allowed to enter the Nebraska riparian strip in the test simulations were present in the modeled corridor width. *Acer saccharinum* was never represented in the riparian strip; *Quercus macrocarpa* entered at 25 years. Relative importance

values from the three modeled corridor widths (10, 20 and 100 m) were calculated. An analysis of variance model, that accounted for the autocorrelation of the years (i.e., the aging of the corridor), was used: 1) to test the importance values for significant differences between the 3 widths (width-only interaction), and 2) to test the importance values for significant differences between the 3 widths at different points in time (width x year interaction).

2.3.1 *Nebraska*

The riparian corridor (a 20-meter strip) was initialized with no trees. Trees were introduced to the landscape based on a visual survey of the number, diameter and location of potential seed source trees in the surrounding area. As noted above, soils were differentiated by their available water content and their depth to the water table. To simulate the effects of encroachment and retreat of cropland, the riparian corridor was decreased to 10 meters and increased to 100 meters, and these simulations were also run for 100 years. The 20-meter width was chosen because it is the actual width of the corridor. The 10-meter width was chosen because it is the smallest width that ***Seedscape*** can model. The 100-meter width was chosen to represent the largest width because it is the maximum observed width of the typical central Great Plains riparian corridor.

2.3.2 *Iowa*

The cutbank edge was initialized to contain the same trees as the interior forest from which it emerged. The cutbank edge was usually one plot (10 meters) wide. Beyond the initial forest composition, it was given the cutbank characteristics (e.g., soils) that captured the greatest diversity of cutbanks observed in the landscape. Like the Nebraska riparian corridor, the simulation was run for 100 years. The landscape was reduced in size due to time constraints

imposed by the large number of plots with seeds to disperse.

2.3.3 *Analysis*

The model data were averaged over the two iterations and all plots. The number of samples (plots x iterations) for the Nebraska 10 meter width is 198. The number of samples for the Nebraska 20 meter width is 396. The number of samples for the Nebraska 100 meter width is 1,980. The number of samples for the Iowa site was 174. The data were averaged because of the uneven sample size between the Nebraska widths and the model and survey data for both sites.

To test the model results against the survey results the individual survey values of relative density, dominance and importance value were subtracted from the modeled values of relative density, dominance and importance values. Model values at 20 years for the 20-meter width were compared with survey values for the Nebraska site. Model values at 100 years were compared with observed values for the Iowa site. Differences between observed and modeled values were examined with a nonparametric test. A student's t value was calculated for testing the hypothesis that the population mean is zero.

An analysis of variance test was constructed to take into account the autocorrelation of the years. It was used to test variation in the response of the importance values to differences in the width of the corridor and to the width of the corridor by year (age) interaction. The importance values were calculated using ***Seedscape*** estimates of numbers and diameters of trees based on simulations at different corridor widths and years.

3. Results

3.1 Model Testing

3.1.1 *Nebraska*

All ten species that were present in the surveyed plots were present in the model results. Two other species (*Acer saccharinum* and *Quercus macrocarpa*) that were present in the landscape outside the surveyed plots had been planted after the riparian corridor was cleared. These two species were initialized at younger-than-seed production age at the start of the simulation to assure that they did not occur in the model results at the beginning of the simulation. Relative density, relative dominance, and relative importance values exhibit similar trends between the model and the survey data. *Populus deltoides* had the largest relative dominance and *Prunus americana* had the largest relative density in the model and survey values (Table 3). *Celtis occidentalis,* was the only species with significantly different importance values between the model result and the survey values (i.e., the differences were significantly different from zero, Table 3). The relative density value differences for *Celtis occidentalis* between the model and survey values were also significantly different from zero. Differences in the relative dominance value of *Populus deltoides* between the model and survey values were significantly different from zero.

3.1.2 *Iowa*

Of the 22 species that were present in the cutbank edge, all except *Zanthoxylum americana* were present in the model results (Table 4). *Zanthoxylum americana* was present in less than half of the survey plots. The model results included *Ostrya virginiana*, which was not present in the cutbank edge.

Though the model included almost all of the species found in the cutbank edge, it was not always successful in capturing the importance values of the species. Differences in importance

values between observed and simulated for nine species were significantly different from zero (Table 4). The nine species were *Tilia americana*, *Quercus velutina*, *Juglans nigra*, *Acer negundo*, *Carya cordiformis*, *Cornus drummondii*, *Morus rubra* , *Morus alba* and *Quercus alba*. Seven species had significantly different relative dominance values between the survey and model data. The seven species were *Carya cordiformis*, *Cornus drummondii*, *Juglans nigra*, *Quercus alba*, *Quercus velutina*, *Tilia americana* and *Ulmus rubra*.

Eleven species had significantly different relative density values between the survey and model data. The eleven species were *Acer negundo*, *Acer saccharinum*, *Carya laciniosa*, *Cercis canadensis*, *Cornus drummondii*, *Morus alba*, *Morus rubra*, *Quercus rubra*, *Quercus velutina*, *Tilia americana* and *Ulmus rubra*.

3.2 *Corridor effects*

3.2.1 *Width effect on importance values*

Populus deltoides had the largest importance value for all three widths over the 100 years (Figures 1-3). *Prunus americana* had the second largest importance value for all three widths until year 35 when *Fraxinus pennsylvanica* had the second largest importance value. Other species that were dominant (as represented by importance value) were *Acer negundo, Quercus macrocarpa,* and *Ulmus rubra*.

Results from the analysis of variance test show only three species (*Juniperus virginiana, Quercus macrocarpa,* and *Salix amygdaloides*) with significant differences ($P < 0.002$) between the importance values for all three widths. Figure 4 shows over the100 years of importance values for *Quercus macrocarpa* that, until year 50, the 20 m width had the lowest importance value, while the values were almost equal for the 10 and 100 m widths. However, after year 55

there was a clear separation in the importance values between the 100m width and the 10 and 20 m widths. At year 80 all three importance values were separated, although at year 100 the 10m and 100m widths were converging.

3.2.2 *Width and year effect on importance values*

Width and year interactions were examined in order to identify possible age-dependent differences in importance values between corridor widths. Only five species had significant differences ($P < 0.05$) for the year and width interaction; they were *Juniperus virginiana, Morus alba, Prunus americana, Salix amygdaloides,* and *Ulmus pumila.* Figure 5 shows for *Prunus americana* that the significance of differences between importance values, especially at the 10 m width, fluctuated widely from year-to-year.

4. DISCUSSION AND CONCLUSIONS

Forest growth models for the Great Plains, hitherto, are not well developed to deal with the strong interactions between agricultural land management practices and forest ecology. Existing models developed for predominantly forested regions do not fit the special landscape features of the Great Plains. This has inhibited the prediction of the ecological effects of agricultural land use change on adjacent shelterbelts and riparian forest zones. Our modified model (***Seedscape***) presents the first example of using spatially explicit, individual-based forest gap models to simulate successional processes in the largely fragmented linear forest types (riparian zones and shelterbelts) of the region.

Our tests suggest that the model performs more realistically in eastern and central Great Plains locations (similar to the Nebraska riparian corridor site) than in the larger forested tracts

common to riparian zones in the western rainfed Corn Belt (similar to the Iowa cutbank site). A potential problem with ***Seedscape*** could be its inability to represent the early death of interior trees caused by the erosion of the cutbank edge into the interior over time; although starting the simulation with a cleared area would also be unrealistic. The model captured the species diversity fairly well. It also captured the relative importance values for half the species found in the cutbank fairly well. Yet, adjustments to the growth parameters for *Populus deltoides,* and to the seed dispersal and the allowable entering number of saplings for *Celtis occidentalis* were needed to make the model perform realistically.

The greater disparity between simulated and observed attributes in Iowa than in Nebraska is attributed to the fact that the model was trained with data from the Nebraska site. That is, the construction of the ***Seedscape*** architecture is based on the characteristics of the Nebraska site which, as noted above, are somewhat different from the Iowa site. For example, flooding at the Iowa site stems mainly from overbank events, not from high-volume overland runoff events typical of the Nebraska site; ***Seedscape's*** reliance on the SCS method rather than local hydrograph data may not capture the relevant hydrological dynamics. Such should be expected to bias the explanatory power of the model toward forested areas sharing characteristics of the Nebraska site. Hence, ***Seedscape***, though not totally without skill in the western Corn Belt, is probably more reliable in the eastern and central Great Plains where corridors are narrower and the edge to area ratio is greater than further east.

The small differences in importance values between the smaller corridor widths (10, 20 meters) are suggestive that seed dispersal from sources outside of the forest is able to penetrate the forest uniformly at those widths. Larger corridor widths may attenuate the penetration of

seeds from outside sources resulting in a distance decay of seeds toward the interior of the corridor. This interpretation may account for the fact that significant differences do emerge over time for some species (e.g., *Quercus macrocarpa*) at the 100-meter width. Hence, a major conclusion of the study is that land use changes which expand corridors to widths that are greater than those currently observed (i.e., greater than 100 meters) can be expected to have measurable influences on biodiversity in the corridors.

A problem with our test of width effects that must be noted is that the disturbance effect of changing the corridor widths to simulate changes in farming practices is done only once, at the start of each simulation. In reality, corridor width changes (contractions and expansions) are likely to occur several times during the course of a 100-year period. This problem is not intrinsic to the model, but rather to the model application protocol. However, based on the assumptions and procedures used in this research, we conclude that simulated changes in corridor widths of Great Plains riparian forests do not seem to have a large effect on successional characteristics of those forests until the widths approach 100 meters. We infer from these results that a trend toward protection of riparian forest strips leading to the growth of corridor widths to 100 meters or greater may have significant effects on biodiversity. Such certainly demands further investigation.

The current version of ***Seedscape*** does not consider seed transport by birds. Avian dispersal of seeds across treeless spaces is one of the important means of species dispersal (e.g, *Juniperus virginiana*). The current version of ***Seedscape*** also has not been modified to account for the effects of large forest edge to width ratios on light penetration into the corridors. We acknowledge these to be important limitations in modeling species composition as a control of

habitat suitability. An interesting topic of future research with ***Seedscape*** is investigation of the effect of an improved light attenuation function on species compostion in the corridor.

The conclusions reached in this study presume the persistence of numerous factors--social and environmental--that are bound to change over long periods of time. The possibility of long-term climate change likely will change processes regulating succession and strongly influence cultivation practices (Easterling, 1996). Present policies aimed at preserving on-farm environmental values are likely to encourage some expansion of forested areas in the Great Plains, but how these policies will fare over the coming decades as pressures mount to increase the production of food and fiber while dealing with climate change is unknown. A range of possible future scenarios must be considered. Future revisions to the model focusing on improvement of the light-attenuation function, added seed dispersal mechanisms, and the scaling of spatially explicit results to the agricultural landscape level are critically needed.

Our analysis suggests that, with improvements discussed above, ***Seedscape*** provides an appropriate tool for tracking the impact of human disturbance change on biodiversity in forests of the Great Plains. Based on our application of the model to the problem of agricultural land dynamics in the Great Plains, a testable hypothesis that a critical forest width must be achieved in order to affect successional processes significantly is suggested.

The ***Seedscape*** model is designed to accommodate these features of forest growth in agricultural landscapes. It was constructed to overcome the limitations of existing forest models for the Great Plains, and to provide a starting point for future developments in understanding ecological processes in heavily human-dominated landscapes. We assert that ***Seedscape*** provides a much-needed tool for assessing the ecological implication of varying the widths of these linear

forest corridors. Wider corridors may provide greater biological diversity than narrow corridors (e.g., Rosenberg et al. 1997), however, economic pressures often encourage agricultural practices that narrow corridors as noted above. A forest model designed for agricultural landscapes may provide a first step in assessing effects of forest corridor width on the diversity of woody plant species.

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Table 1. Species-specific reproductive parameters and dispersal agents. SAP is the maximum number of saplings added per year. Age_{min} and Age_{max} are the minimum and maximum ages at which a tree can produce seeds. $Pr_{(seeds)}$ is the probability that a tree will produce seeds in a given year. Values for dispersal agents are given in Table 2.

Species	SAP	Age_{min}	Age_{max}	$Pr_{(seeds)}$	Dispersal agent	
					Primary	Secondary
Acer negundo	3	30	100	1.0	1	
Acer saccharinum	2	35	125	1.0	1	
Carya cordiformis	2	30	175	0.3	8	
Carya illinoensis	2	20	300	0.8	5	8
Carya laciniosa	2	40	350	0.8	5	7
Celtis occidentalis	3	35	200	0.8	5	7
Cercis canadensis	10	7	90	0.6	1	5
Cornus drummondii	20	15	100	1.0	5	7
Craataegus spp.	5	10	125	0.9	5	1
Fraxinus pennsylvanica	10	15	150	0.8	2	8
Gleditsia triacanthos	3	10	100	0.9	5	8
Gymnocladus dioicus	3	10	100	0.9	5	8
Juglans nigra	3	12	80	0.2	5	8
Juniperus virginiana	3	10	150	0.8	6	
Morus alba	3	5	125	1.0	6	
Morus rubra	3	5	125	1.0	6	
Quercus alba	10	30	150	0.3	5	6
Quercus macrocarpa	10	25	250	0.5	5	6
Quercus rubra	10	25	125	0.3	5	6
Quercus velutina	5	20	100	0.5	5	6
Populus deltoides	10	25	150	0.9	4	7
Prunus americana	60	10	40	1.0	5	7
Salix amygdaloides	10	10	85	0.9	4	
Tilia arnericana	5	15	140	0.8	1	5
Ulmus americana	3	15	300	0.5	2	
Ulmus pumila	15	15	70	0.5	2	
Ulmus rubra	3	15	200	0.5	2	
Zanthoxylum americanum	20	15	50	0.5	1	5

Table 2. Values of φ for each dispersal agent used in dispersal equation. Dispersal agents are based on Malanson and Armstrong, 1996.

Dispersal agent	i	Φ
Wind (short distance)	1	1.07
Wind (intermediate)	2	1.04
Wind (intermediate)	3	1.01
Wind (long-distance)	4	0.90
Mammal	5	1.02
Bird (blue jay)	6	0.94
Bird (other)	7	0.99
Gravity	8	10000.00

Table 3. Mean and standard deviation (sd) of relative density, relative dominance and relative importance values for model and survey data from the Mead riparian corridor. The differences between model and survey results were tested using t-tests.

Species	Relative Density (%)				Relative dominance (%)				Relative importance (%)			
	model		survey		model		Survey		model		survey	
	mean	sd	mean	sd	mean	sd	Mean	sd	mean	sd	mean	sd
Acer negundo	6.51	4.21	2.84	6.62	0.87	1.07	1.43	7.95	7.38	4.74	4.27	14.58
Celtis occidentalis	3.25	2.32	0.71*	1.65	0.00	0.00	0.03	0.20	3.25	2.32	0.74*	1.86
Fraxinus pennsylvanica	24.05	9.95	8.51	25.63	0.79	0.85	5.40	10.91	24.84	10.28	13.91	36.54
Juniperus virginiana	2.21	1.63	1.42	4.71	0.07	0.12	0.23	0.47	2.28	1.67	1.65	5.18
Morus alba	3.65	2.73	19.15	30.78	0.06	0.54	19.67	33.87	3.71	2.84	38.82	64.51
Populus deltoides	9.21	5.10	12.77	19.02	95.96	3.63	42.02*	39.34	105.17	7.52	54.79	57.72
Prunus americana	42.59	15.70	42.55	26.28	0.38	1.73	6.50	25.26	42.97	16.09	49.05	47.56
Salix amygdaloides	3.17	2.06	9.22	10.39	0.97	2.70	22.10	30.40	4.14	3.56	31.32	38.88
Ulmus pumila	1.96	1.72	0.71	1.94	0.87	1.21	2.15	5.68	2.83	2.66	2.86	7.63
Ulmus rubra	3.40	2.68	2.12	3.35	0.03	0.11	0.47	1.31	3.43	2.72	2.59	4.66

* $P < 0.05$

Table 4. Mean and standard deviation (sd) of relative density, relative dominance and relative importance values for model and survey data from the Iowa cutbank edge. The differences between model and survey results were tested using t-tests.

Species	Relative Density (%)				Relative Dominance (%)				Relative Importance (%)			
	Model		Survey		Model		Survey		Model		Survey	
	mean	sd	Mean	sd	mean	sd	Mean	sd	mean	sd	mean	sd
Acer negundo	17.39	7.48	1.51***	7.90	6.17	8.82	3.24	4.49	23.56	13.17	4.75***	9.54
Acer saccharinum	8.73	4.40	0.48**	6.07	2.59	4.49	14.39	25.04	11.32	6.28	14.87	31.10
Carya cordiformis	11.73	8.78	6.99	9.32	25.43	16.07	3.06***	3.50	37.16	18.46	10.1***	12.41
Carya illinoenis	0.20	0.20	0.60	1.57	0.04	0.22	2.49	4.92	0.24	0.17	3.09	6.22
Carya laciniosa	4.36	3.39	0.84*	3.34	5.92	8.77	4.75	11.29	10.28	9.61	5.59	13.70
Celtis occidentalis	4.81	4.39	13.68	14.54	4.80	10.40	16.45	19.40	9.61	12.39	30.13	30.93
Cercis canadensis	11.34	5.82	3.50***	4.08	0.02	0.11	4.40	8.85	11.36	5.86	7.90	12.66
Cornus drummondii	1.46	3.93	42.4***	23.22	0.01	0.25	3.56**	3.96	1.47	3.13	46.0***	26.01
Craataegus spp.	0.15	0.18	0.66	0.66	0.03	0.21	0.42	1.17	0.18	0.19	1.08	1.81
Fraxinus pennsylvanica	0.10	0.18	1.75	5.89	0.03	0.48	6.51	17.29	0.13	0.48	8.26	18.25
Gleditsia triacanthos	0.05	0.03	0.36	1.32	0.00	0.00	4.92	14.03	0.05	0.00	5.28	15.36
Gymnocladus dioicus	0.02	0.00	0.24	0.39	0.00	0.00	0.17	0.57	0.02	0.00	0.41	0.95
Juglans nigra	1.13	3.13	0.18	1.26	14.92	9.41	2.24**	9.80	16.05	10.45	2.42**	11.07
Morus alba	2.33	1.74	0.12***	0.37	0.03	0.17	0.06*	0.15	2.36	1.78	0.18***	0.47

Morus rubra	3.97	2.26	0.48***	0.51	0.07	0.20	0.46	1.22	4.04	2.26	0.94***	1.64
Quercus alba	2.83	4.21	2.11	2.18	23.02	9.89	8.18	14.60	25.85	9.25	10.29*	14.29
Quercus rubra	1.66	2.39	0.30***	0.45	0.15	0.39	2.10	3.27	1.81	2.50	2.40	3.67
Quercus velutina	3.71	3.13	0.12***	0.15	13.59	16.11	1.55***	6.62	17.30	16.19	1.67***	6.77
Tilia arnericana	4.38	2.58	0.06***	0.14	0.07	0.46	0.01***	0.01	4.45	2.62	0.07***	0.15
Ulmus americana	0.08	0.21	0.36	0.71	0.00	0.00	0.66	1.03	0.08	0.13	1.02	1.74
Ulmus rubra	13.57	5.96	4.40***	4.54	3.04	5.28	19.88*	19.99	16.41	9.27	24.28	21.79
Zanthoxylum americanum	0.00	0.00	18.81	24.92	0.00	0.00	0.50	1.43	0.00	0.00	19.31	26.20

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

FIGURE LEGENDS

Figure 1. Relative importance values in percent for each species for the three model corridor widths for year 20.

Figure 2. Relative importance values in percent for each species for the three model corridor widths for year 60.

Figure 3. Relative importance values in percent for each species for the three model corridor widths for year 100.

Figure 4. Relative importance values in percent for *Quercus macrocarpa* for the three model corridor widths for 100 years.

Figure 5. Relative importance values in percent for *Prunus americana* for the three model corridor widths for 100 years.

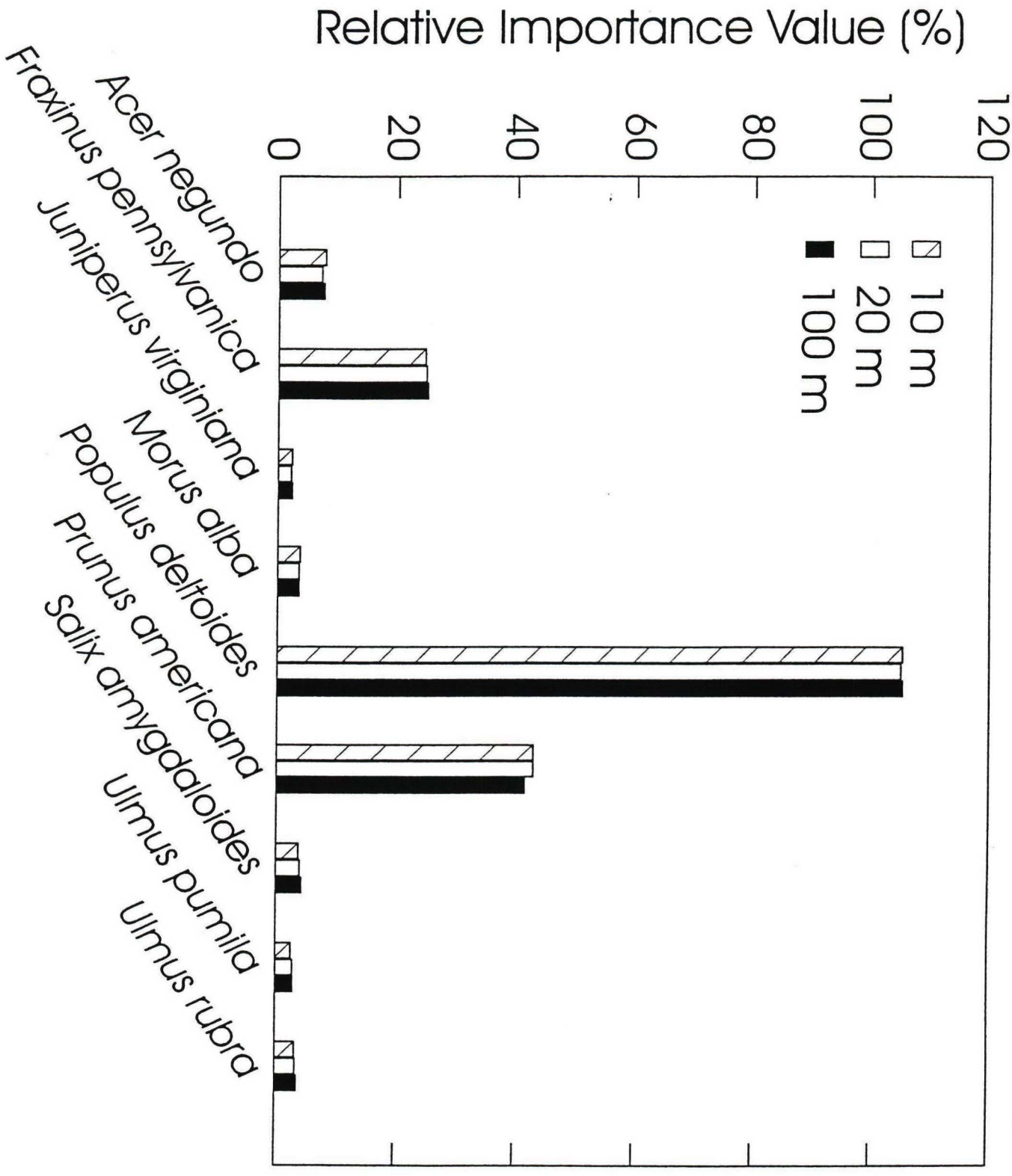

Figure #1
Easterling et al.

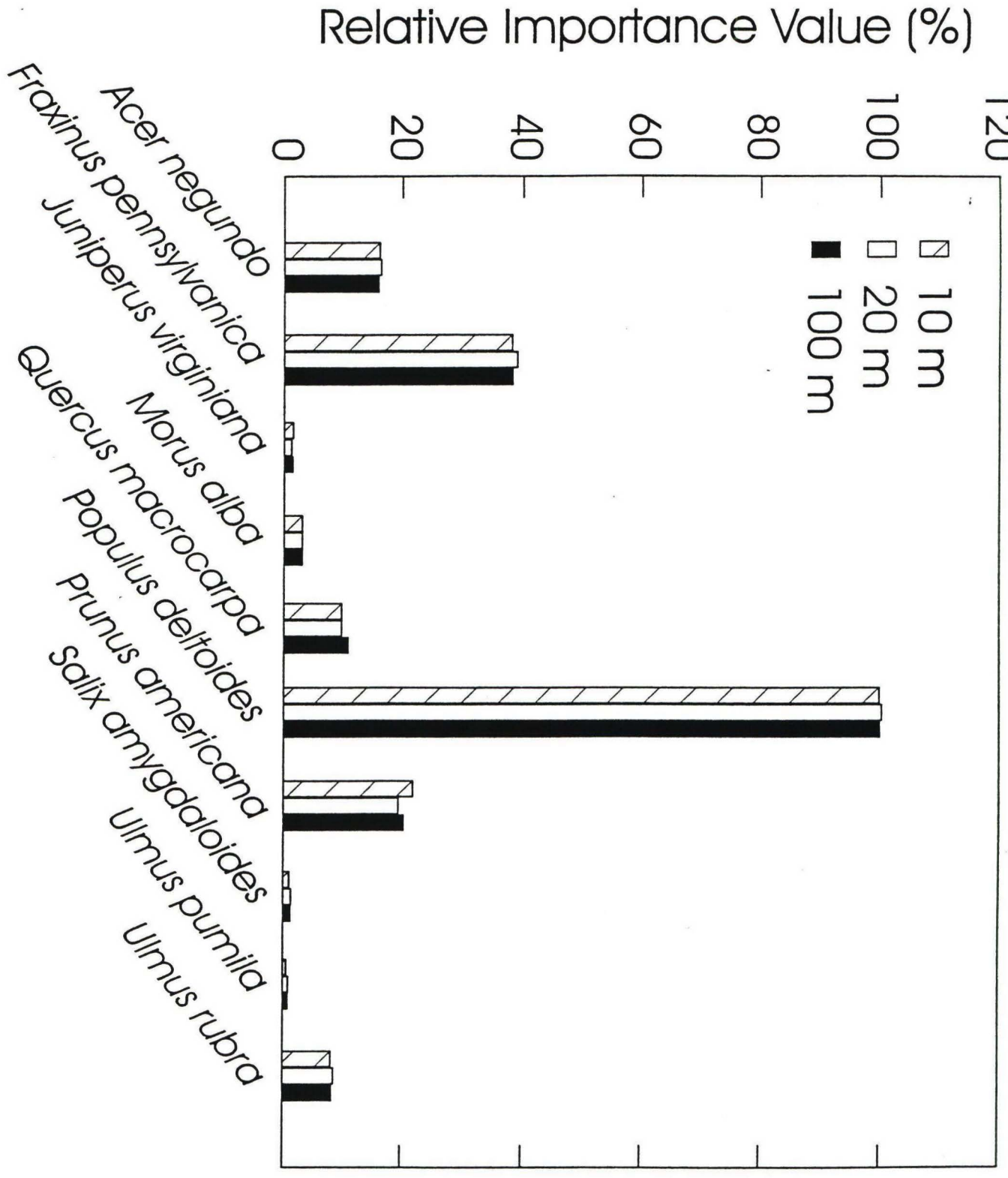

Figure #2
Easterling et al.

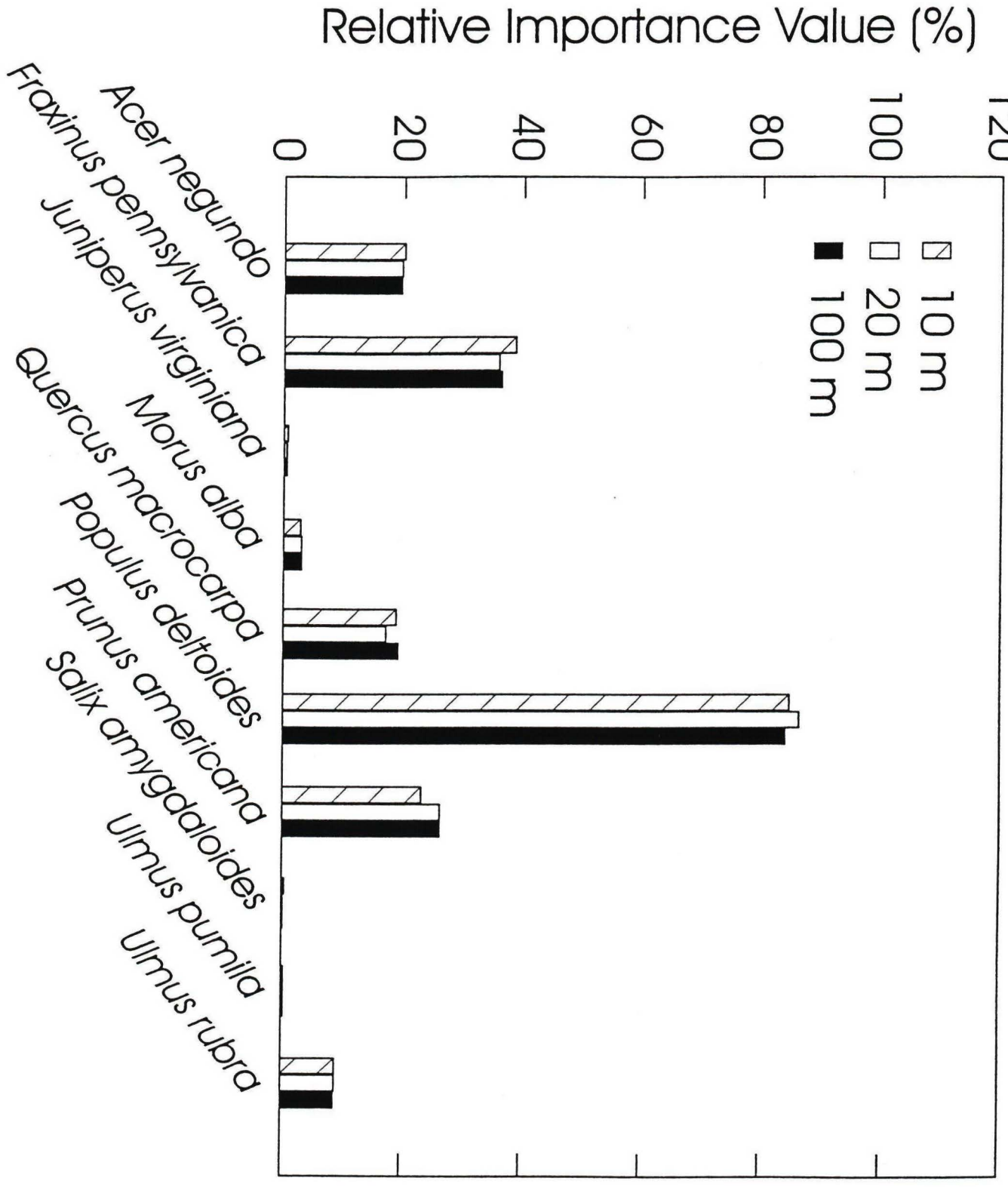

Figure #3
Easterling et al.

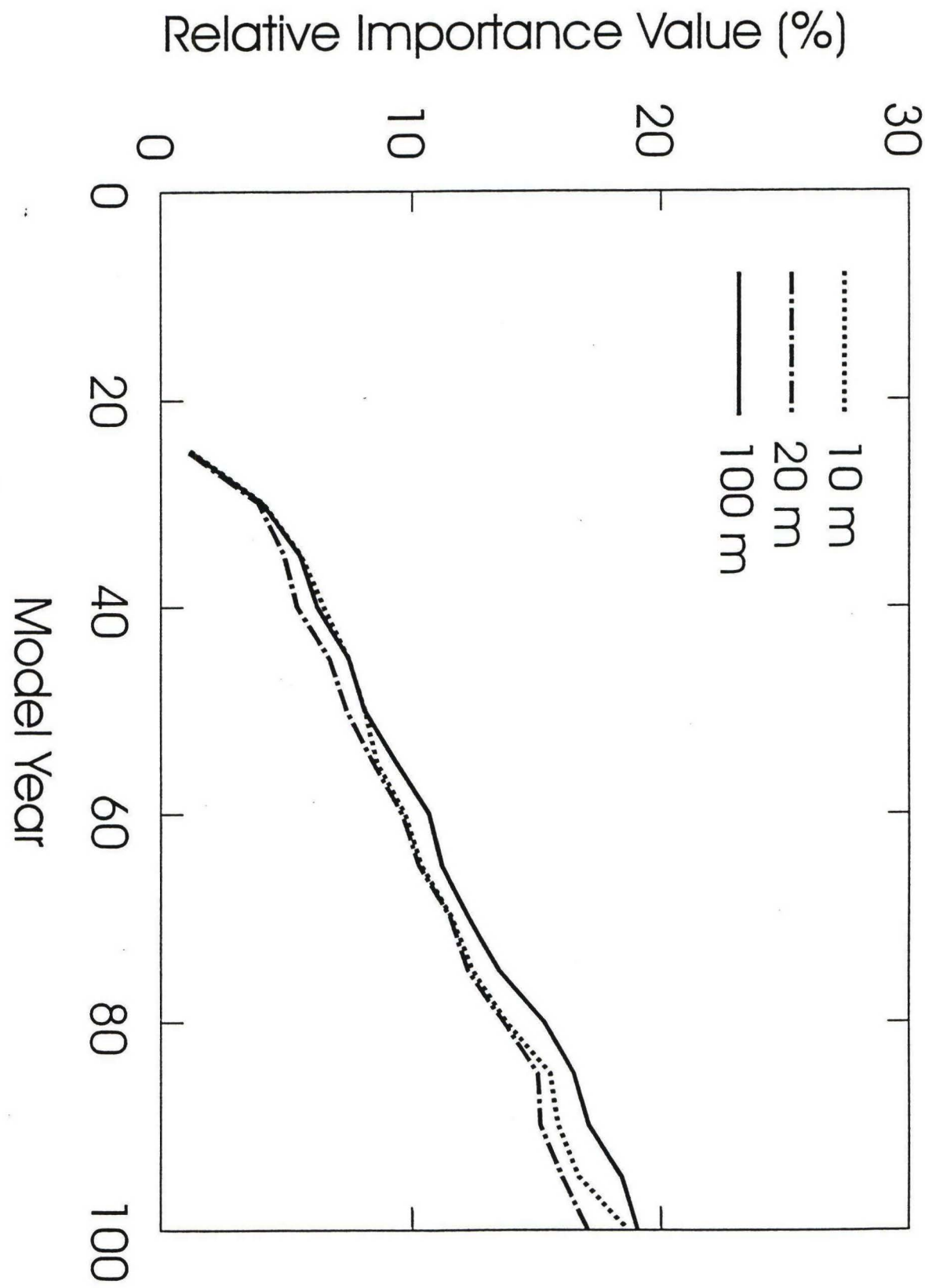

Figure #4
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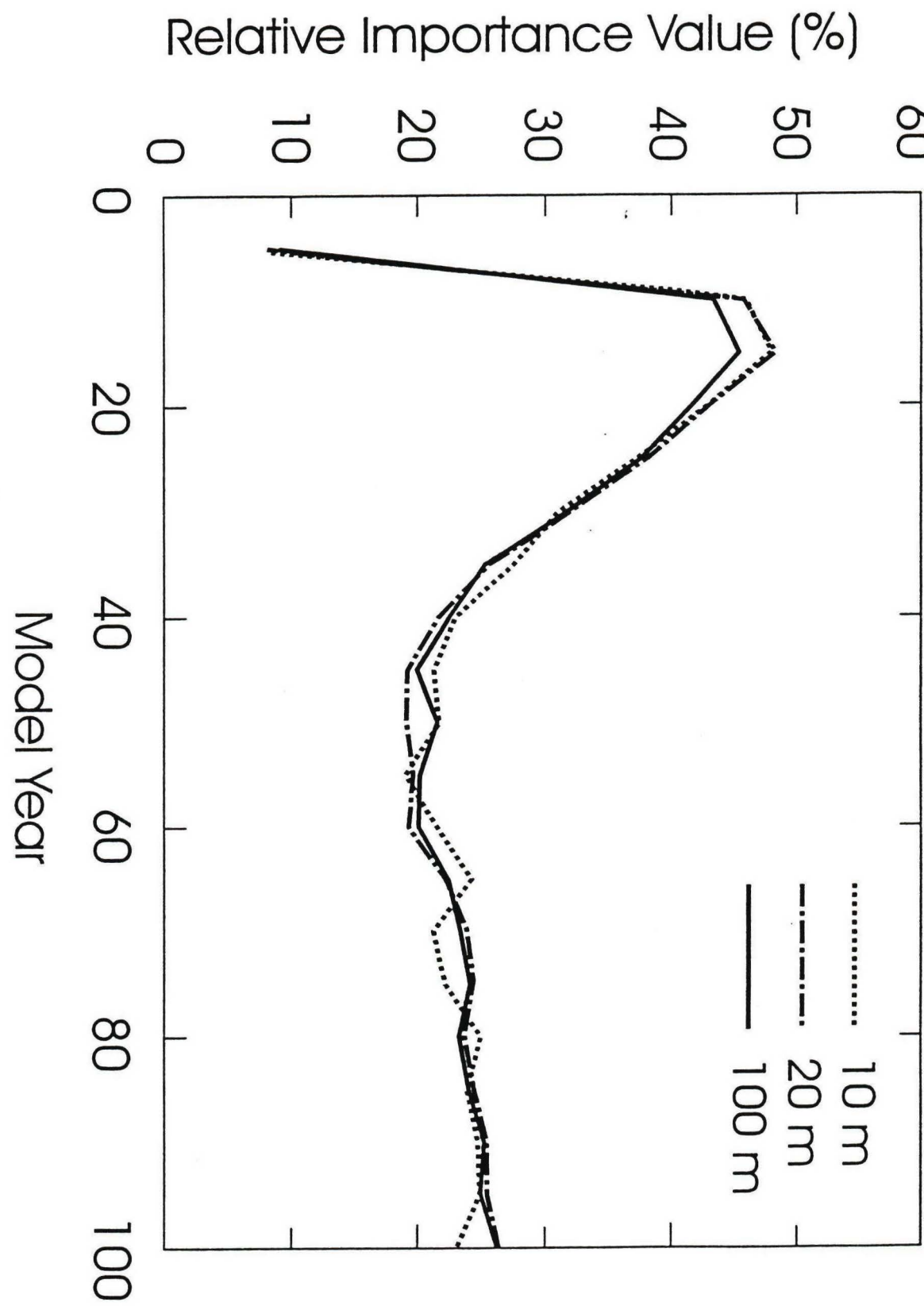

Figure #5
Easterling et al.

SPATIAL-TEMPORAL POPULATION DYNAMICS ACROSS SPECIES' RANGE: FROM CENTER TO MARGIN

by

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Abstract. Understanding the boundaries of species' ranges and the variations in population dynamics from the center to margin of a species' range is critical. This study simulated spatial-temporal patterns of birth and death rates and migration across a species' range in different seasons. Our results demonstrated the importance of dispersal and migration in altering birth and death rates, balancing "source" and "sink" habitats, and governing expansion or contraction of species' ranges in changing environments. We also showed that the multiple equilibria of metapopulations across a species' range could be easily broken following climatic changes or local or regional physical disturbances. Although we refer to our models as describing the population dynamics across whole species' range, they should also apply to small-scale habitats (metapopulations) in which species abundance follows a Gaussian pattern or to any ecosystem or landscape where strong central-marginal (C-M) environmental gradients exist. Conservation of both central and marginal populations would therefore be equally important considerations in making management decisions.

Keywords: central-marginal gradient; dispersal; migration; spatiotemporal population dynamics; species' range.

INTRODUCTION

Population density tends to be highest near the center of a species' geographical range and declines gradually toward the boundaries (Fig. 1; Whittaker 1956, Westman 1980, Hengeveld and Haeck 1982, Brown 1984, Maurer and Brown 1989; but see Brussard 1984). This spatial pattern, modeled well by a Gaussian distribution, may occur at any scale, ranging from a patch to the entire species' range (Brown 1984). Although this pattern has been intensively studied (e.g. Pielou 1969, Greig-Smith 1979), a number of questions regarding the underlying mechanisms that control population dynamics (i.e., birth and death rates and migration) remain unanswered (Carter and Prince 1981). Most previous theoretical and empirical studies on population dynamics focused only on the temporal patterns of local populations, with little attention paid to the differences in birth and death rates in different habitats and migration rates across habitats within the species' range (Green 1989, Renshaw 1995, but see Hanski 1982, Pulliam 1988, Howe et al. 1991). Further, recent studies either examined the dynamics of marginal populations (e.g., Holt 1983) or compared the characteristics of central and marginal populations (e.g., Soulé 1973, Tabachnick and Powell 1977, Grant and Antonovics 1978, Brown 1984, Brussard 1984) with no effort made to link central and marginal populations in terms of spatial changes in birth and death rates or dispersal and migration across central-marginal (C-M) gradients (Pulliam 1988). It is unclear how these spatial differences in birth and death rates within a species' range can be altered by dispersal or migration (Johst and Brandl 1997).

To maintain the bell-shaped distribution, a corresponding population regulation must be operating in the system (Berryman 1981), with environmental gradients from a species' range

center toward margin significantly affecting the population regulation (Linhart 1974, Grant and Antonovics 1978, Brussard 1984). In central or "source" habitats, the reproductive rate may exceed the mortality rate, while the opposite may occur in marginal or "sink" habitats (e.g., Pulliam 1988, Howe et al. 1991). However, empirical evidence suggests that populations with different mobilities (or dispersal powers) have different mechanisms regulating population density below or approaching the carrying capacity across the species' range (e.g., Grant 1978, Guo et al. 2000). For example, in most plant populations, dispersal is limited and the rates of birth (*b*) and death (*d*) may be the major factors regulating population density. Under this scenario, migration is controlled by the local changes in birth and death rates. In contrast, animal populations are predominantly influenced by the dispersal and migration decisions of individuals, making the spatial distributions of these populations more sensitive to environmental changes. Hence, dispersal and migration play more critical roles in adjusting local population densities and spatial distributions (e.g., Primack 1996).

To better understand the patterns of species distribution, it is necessary to monitor both temporal and spatial variation of population dynamics throughout the species' range (Pease et al. 1989, Hengeveld 1990). In this study, we examined population regulations along environmental gradients through the species' range from the center toward the margins. We asked (1) how do birth and death rates and migration change across a species' range from center to margin and through time; (2) how do spatial environmental gradients affect population regulation and density; and (3) how do spatial and temporal population regulations along C-M gradients affect the species' range dynamics?

GAUSSIAN DISTRIBUTION AND IMPLICATIONS

In general, the most favorable conditions are found at the center of a species' distribution, and these conditions support the highest population density (Whittaker 1956, 1967, Brussard 1984). With increasing distance away from the center in any direction, one or more variables become less favorable, leading to a decrease in population densities. If environmental variation in the limiting factors are reasonably gradual, the spatial distribution of population density along any transect which runs through the center of the species' ranges will tend to resemble a bell-shaped surface (Brown 1984, Whittaker 1967, Westman 1980):

$$N = ae^{-cx^2} \qquad (1)$$

where N is population density, a and c are species-specific constants, and x is the distance from the center of the species' range (Fig. 1a).

It has been argued that the population density change is regulated by the physiological tolerances of a species and altered by resource competition with coexisting species (Westman 1980). Since population density decreases from center to margin, the regulation of population dynamics from center to margin could switch from density-dependent processes (K-selection) to density-independent processes (r-selection). Therefore, a species occupancy of its range margin would be determined by immigration, by physical stress, and by the outcome of various interspecific interactions (Davis et al. 1998). In the absence of interspecific competition, a species could reach its maximum abundance at the center of its environmental range where strong intraspecific competition occurs (Fig. 1a). As its abundance declines toward the extremes

of its tolerance at the range margin, however, density may be strongly affected by biotic interactions with other species (e.g., competitors, predators; see Grant and Antonovics 1978). The relative strength of intraspecific competition (i.e., a value in equation 1) and the interspecific competition (i.e., c value) control the height and flatness of the Gaussian curve (Fig. 1a).

Empirical studies have shown that not only do central habitats hold higher population densities, but they also maintain greater genetic diversity (Parsons 1991). According to Barton (1985), we would also expect more gene flow into the less fit populations (asymmetric gene flow; see also Pulliam 1988). Thus central populations may be less sensitive to environmental fluctuations because in different years with different environments, alternative genotypes of the species would be favored (Carson 1956, Mayr 1963, Soulé 1973).

THE MODEL

We constructed a model by first dividing a species range into numerous rings (patches) surrounding the center of the species' distribution (Fig. 1b). We assumed physical conditions were homogeneous and population parameters were spatially constant within each ring. All patches were then connected from center to margin as a gradient to simulate the spatial variation of population parameters along the gradient. The variation in population density from the species' range center to margin was assumed to follow a Gaussian distribution.

The population growth rate in the whole jth ring, r_j, is:

$$r_j = b_j - d_j + i_j - e_j \qquad (2)$$

where b and d are birth and death rates and i and e are immigration and emigration rates, respectively. If the population is locally stable, i.e., at equilibrium, then, $r_j = 0$. The habitat is a "source" if $(i_j - e_j) < 0$. It is a "sink" if $(i_j - e_j) > 0$. Similarly, for an equilibrium to occur globally within the species' range, the overall population growth rate of the species ($\boldsymbol{R}$) is

$$\boldsymbol{R = B - D + I - E = 0} \qquad (3)$$

where $\boldsymbol{B}$, $\boldsymbol{D}$, $\boldsymbol{I}$ and $\boldsymbol{E}$ are total birth and death rates as well as migration in all populations of the species in question. For values of $\boldsymbol{R} > 0$, the species' range is assumed to be expanding; if $\boldsymbol{R} \leq 0$, the range is considered to be stable or contracting.

The set of equilibrium points (i.e., when population gain equals loss) for the population in space determines the general pattern of population abundance. However, in natural dynamic systems, the values of the four parameters are rarely balanced. The equilibrium point will therefore never truly exist under changing environments (Maurer and Brown 1989, Hanski et al. 1995). Instead. if environmental conditions are fluctuating stochastically, populations will attain what is known as a stationary distribution in both space and time. In the following sections, we will discuss the above parameters with special attention paid to the effects of dispersal and migration on population regulation and dynamics.

A major feature in most plant populations is that migration can be governed only by altering birth and death rates at different locations following the migration trends (Maurer and Brown 1989). Levin (1984) has defined immigration rate in plant populations as the ratio of the number of alien pollen and seeds to the total number of pollen and seeds in a local population.

The greater the local pollen and seed production, the lower the immigration rate will be. Empirical studies suggest that a plant mainly deposits seeds and pollen locally, i.e., in neighboring habitats. It was assumed that emigration was deposited only into the adjacent rings and migration occurs only across neighboring rings in random directions (Fig. 1b; Levin and Kerster 1974, Grant and Antonovics 1978, Levin 1988, Greene and Johnson 1989, Okubo and Levin 1989, Menges 1991). Thus, based on Levin's arguments and Gaussian patterns of habitat carrying capacity within a species' range, the maximum birth, death, and migration rates under optimum conditions from center toward margin were calculated.

In contrast to plants, an important characteristic of most animal populations is their active movement, which makes migration many times more efficient. Birth rate, as well as death rate, can be effectively adjusted by migration. In addition, high population density at the range center may restrict immigration and promote emigration in order to reduce the strong intraspecific competition (Stacey et al. 1997). Furthermore, animal dispersal or migration may be more long range and directional compared to that of plant populations (Primack 1996). The assumption follows that each individual can immigrate everywhere within its range until a favorable habitat is reached, making per capita birth rate intrinsic and less density-dependent. However, as discussed later, migration becomes highly critical at the species' range margin where fragmentation of habitat leads to higher extinction probabilities (Forney and Gilpin 1989).

According to Pulliam (1988), habitats near the center serve as "sources," while those near the margin will be "sinks." The population parameters therefore should have the following variation within a species' range:

$b_{j-1} > b_j > b_{j+1}$, and $d_{j-1} < d_j < d_{j+1}$,

$i_{j-1} < i_j < i_{j+1}$, and $e_{j-1} > e_j > e_{j+1}$.

For the same reason, survivorship should have a distribution similar to birth rate. In other words. the death rate should be less density-dependent in populations of species with high dispersal power and this density dependence should be transferred to density dependence in immigration and emigration. The population regulation processes that govern the number of individuals leaving and entering each ring can be subdivided into a density-dependent birth and death process (see Shigesada and Roughgarden 1982), and a density-dependent emigration and immigration process. Because internal environmental conditions determine the intensity of competition. it also controls the migration of individuals in or out of the ring. Therefore, the movement of individuals in response to the environment is an intrinsic feature of the model.

Population regulation often refers to the ability to decrease the population size when it is above a particular level (carrying capacity), and to allow an increase in the population size if it is below that level. This particular level or carrying capacity should therefore be a point of equilibrium (Begon and Mortimer 1986). When population size reaches the habitat carrying capacity, such as under equilibrium conditions, there are four major regulation cases. First, birth and death rates rate are equal in each ring (whether they are density-dependent or not); in this case, dispersal and migration rates are density-independent and will play a minimum role in spatial-temporal variation of population dynamics. This is true for most sessile organisms. Second, birth rate follows the bell-shaped pattern (decreases from center to margin) but death rate is density-independent. Third, birth rate is density-independent but death rate follows the

bell-shaped pattern (increases from center to margin). In these two case, migration from central habitats to marginal habitats will occur (Fig. 2). Last, birth and death rates are not equally density-dependent, and dispersal and migration will still play a significant role in population regulation. In all cases, the birth and death rates and dispersal and migration mutually influence each other and regulate population size.

SIMULATION RESULTS

Effects of dispersal and migration

The effects of dispersal and migration on population regulation and source-sink habitats are illustrated in Fig. 3 (migration rates). {{If a species (e.g., a new emerging species or newly introduced species) is under mass expansion, its birth rate could well exceed death rate across the whole species range until such expansion stops. Conversely, if a species's range is contracting (e.g.. toward extinction), the death rate will exceed the birth rate across the whole range although the deference between birth and death rates could be different across the species range. Without dispersal or migration and at the equilibrium, birth rate and death rate must be balanced, no matter what shapes the birth or death curves might be.}} This might be the case for populations of many plant species. Otherwise, birth rates exceeding death rates will cause a mass emigration through dispersal from central habitats (i.e., sources) to marginal habitats (i.e., sinks). This is probably the case for most animal populations (Fig. 4). {{In either case, the actual abundance curve of a species may indicate the migration direction of a species under environmental changes (e.g., global warming). Fig. 5 is an example of such migration tendency that the species is moving in a certain direction where ***R*** is higher on one side than the other

side.}} Source and sink habitats can be easily identified in the seasonal migration map (Fig. 6).

In plant populations, because of their limited dispersal power, migration only occurs across neighboring habitats and therefore the population size is mainly controlled by birth and death rates. In animal populations, however, the birth and death rates can be less density-dependent because of their greater dispersal power. {{However, there are exceptions in the real world. Some plant species have extremely high dispersal power so they may behave like most animal species, and some animal species have very low mobility so they may actually behave like most plant species in terms of dispersal or migration ability}}.

C-M population dynamics

Although population density across the species' range follows Gaussian distribution (Fig. 1a and equation 1), the rings in the middle range along the C-M gradients were found to hold the largest total population size, N_j (Fig. 7):

$$N_j = n_j \pi (x_{j+1}^2 - x_j^2) \qquad (4)$$

where n_j is the population density in jth ring which follows Gaussian distribution, and x_j is the distance of jth ring to the center of the species' range.

Simulations of this model produced pictures of spatial-temporal population dynamics along the C-M gradients (Fig. 8). The species distribution boundaries fluctuate with short-term, usually cyclic environmental changes. Year-to-year precipitation or temperature variations often produce small or local habitat expansions or contractions within the species' range (Levin 1984,

Maurer and Brown 1989). Animal species showed higher degrees of range fluctuation under environmental variation than plants. However, long-term environmental changes will have more dramatic effects on the whole species' range, causing long-distance species migration for both plants and animals.

The habitat suitability also changed through time during population development. Suitability of internal range for further population growth decreased while suitability of peripheral rings increased. Fig. 8 displays how population density changes over time (reproductive seasons) across rings from center to margin. When population density was well below the carrying capacity (density-independent), central rings were most favorable. As population size increases and fluctuates around carrying capacity (density-dependent), as a result of high birth rate and low death rate, the habitat will become less favorable. By this time, the next ring becomes more favorable. {{Therefore, in corresponding to dramatic environmental changes, we may observe that the same habitats serve as both "sources" and "sinks" in different times or the switches of "sources" and "sinks" at the same locations over time.}}

Sensitivity analysis showed that central populations are more stable, both spatially and temporally and {{animal populations are more sensitive to stochastic environmental changes than plant populations, given the similar population sizes and time frames (Fig. 9)}}. In both plants and animals, marginal populations are more sensitive to environmental changes and vary among species depending on the dispersal power or migration ability of particular species. Populations of species with greater dispersal power or migration rates are more sensitive than those with poor dispersal power.

DISCUSSION

Different patches of a species' range vary in terms of resource availability or carrying capacity and therefore in their suitability for use by an organism. It follows that environmental patches arranged from center to margin play an important role in influencing spatial-temporal population dynamics (Shorrocks and Swingland 1990). A common feature shared by all species is that central populations, as compared to marginal populations, are less sensitive to environmental change due to their larger population size (cf. Grant and Antonovics 1978). When environmental conditions change, the organism can avoid extinction either by adapting genetically to the new environmental condition, or by tracking its old environment across space (Pease et al. 1989). Because of the general low vagility of plants, it is likely that plants will tend to genetically adapt to environmental changes. On the other hand, animals with their greater vagility are more likely to respond to environmental change by tracking their favored environment across space. The mechanisms of species response to persistent environmental change will be a critical issue in the near future as global change intensifies.

C-M gradients

Marginal populations are believed to be more isolated and suffer higher extinction risks than central populations. However, demographic and genetic contributions from conspecific immigrants tend to reduce extinction rates of insular populations. This phenomenon is referred to as the "rescue effect" (Brown and Kodric-Brown 1977, see also Pulliam 1988, Stacey et al. 1997). Populations in marginal habitats may thus be sustained partially by a net outflow from central populations. Apparently, this process is integral to metapopulation persistence. Island

biogeography theory may also apply to metapopulations, especially when the variations in patch size and isolation level from center toward margin are considered. The marginal habitats inhabited by a species are often smaller in area, more fragmented, and, therefore, more isolated, despite the general central-marginal migration trend. This isolation can increase in times of environmental change. Because of their supposedly unique genetic properties, marginal populations are considered very important in speciation events (Bush 1975, Brussard 1984).

In the simplest case of undirected movement, emigrants may travel equally in all directions (Fig. 1b). Directed movements across one or two boundaries may occur if the local or whole range of the species is considered. In either case, the net result of the migration process will usually be a movement of organisms from the crowded rings into the less crowded ones.

The present models show that the birth and death rates per capita in plant populations are the most important factors. Dispersal and migration are only important locally, and its dynamics are governed by the processes controlling births and deaths. When the population reaches the habitat carrying capacity, high birth rate will be prohibited; otherwise, the death rate should be correspondingly high. Empirical data seem to support this conclusion (Grant and Antonovics 1978). In animal populations, the global environmental conditions within a species' range control population dynamics due to the animal's active habitat selection (Pulliam 1988).

The net migration of individuals (immigration and emigration) is the determining factor influencing species migration, range expansion/contraction, or extinction. Very high population density due to high birth rate may be reduced by emigration. Hence, emigration acts to spread the population over its range, and to moderate the density of the population in any particular part of the range, and to reduce the impact of density-dependence on local birth and death rates.

Once immigrants have entered a ring, they may pass through the population growth process if they are reproductively mature, but they would have different demographic characteristics compared to those they would have had in the "home" ring. For example, the reproductive ability may be lower and death rate may be higher.

The cause of the above difference between plant and animal populations is due, to a large extent, to the different vagilities and propensities for directed motion of these taxa. In plant populations, seeds, spores, and pollen can migrate in relatively random directions and mostly locally, whereas animals with active habitat selection can migrate long distances and typically toward more favorable patches (in this sense, i.e. less crowded patches).

When we consider the population over its entire range, the only processes governing its numerical dynamics are the birth and death rates. However, when we focus on the species' range margin to predict the expansion or contraction or the direction of range migration, the four population parameters (*b, d, i, e*) all play important and different roles in these processes. A plant species' range expansion, contraction, or migration is mainly induced by the differential birth (seed immigration and seedling establishment) and death rates in different parts or neighboring areas of the range, whereas a change in an animal's range may be controlled largely by the movements of mature individuals. What we have set up as a dichotomy will actually be a continuum with range dynamics controlled largely by the mobility of the focal species. For a less mobile animal species', change in its range may be controlled by mechanisms similar to plant species' range changes.

Effects of dispersal/migration

It is critical to understand the role of dispersal and migration in population regulation along C-M environmental gradients. Less mobile populations (mostly plants) would show slow-paced migration following climate change. Once populations of species with poor dispersal ability reach the habitat carrying capacity, density-dependent processes would limit birth rate or increase death rate. On the other hand, in mobile populations, local birth and death rates may be less density-dependent due to the mobility of its individuals. In general, at the center of the range higher birth rate may result in emigration to support the marginal populations where within-habitat reproduction is insufficient to balance locally higher mortality. As a consequence, populations may persist in such habitats, being locally maintained by continued immigration from the species' range center where reproductivity is high and mortality is low. The distribution of mobile organisms may be more sensitive to environmental changes than those of immobile ones. Empirical data seem to support our simulation predictions (e.g., Grant and Antonovics 1978).

In many cases, distribution boundaries are not limited by physical factors such as climate, instead, they are limited by dispersal power or interactions with other species (Hutchinson 1959). This is demonstrated by the success of plants transplanted by humans all over the world. Interestingly, the proportion of successful animal transplantation is lower than that of plants (see Williamson 1996). Thus, we suspect that the range boundaries of species with greater dispersal or migrational power are more climatically controlled, whereas others are more limited by their dispersal or migration ability.

Exodus from a particular environment usually occurs when resources are depleted or when the environment becomes intolerable because of physical conditions or the presence of

other organisms (competitors, predators, or pathogens). In the short term, marginal plant populations can persist through vegetative growth (Olesen 1987) or autogamy (Stebbins 1950, Jain 1976). However, in the long run, marginal populations can persist only through immigration from central or "source" habitats (Brown and Kodric-Brown 1977, Pulliam 1988, Howe et al. 1991). Therefore, dispersal or migration is extremely important for those species that denude their resources or that inhabit highly variable environments. It is not surprising, therefore, that animals with highly developed dispersal powers, such as birds or insects, have been most successful in utilizing rare or temporary habitats, and many organisms have developed higher dispersal ability in marginal patches (Brussard 1984). In contrast, organisms inhabiting consistently favorable environments (i.e., central habitats) tend to be less mobile (Brussard 1984). However, organisms without good dispersal powers cannot afford to overexploit their environments and must, therefore, practice conservation by limiting their own numbers through controlling birth rate or death rate (Berryman 1981). Territorial behavior is one of the most successful tactics for achieving these ends.

On the other hand, density-dependent factors may play different roles in different populations with various dispersal powers. In populations with lower dispersal or migration rates, such as most plant populations, higher intraspecific competition results in higher death rates rather than mass migration. In contrast, in most animal populations, higher intraspecific competition would cause higher emigration rates from crowded habitats (Stacey et al. 1997). Animals' mobility makes migration much more efficient, and birth and death rates can be effectively altered by migration. Intra- or interspecific aggressiveness has an important function in stimulating migration. If, however, migration is inhibited, this same aggressiveness may

cause local mortality through different ways or reduce local reproduction (birth rate). Thus, interspecific competition may be one of major forces controlling the species' range limitation (e.g., Davis et al. 1998).

Population regulations and species' range dynamics

The variations of population dynamics across a species' range are closely related to the dynamics of the species' range, i.e., expanding, contracting, or migrating. In responding to temporal environmental change, plant and animal populations have very different responses. In animal populations, migration is more sensitive to environmental variation, and the density should be highly correlated with prevailing seasonal and annual environmental regimes. In plant populations, birth and death rates are more sensitive than migration. The shorter the longevity of the species, the quicker the species will respond. For example, annual plant density may be sensitive to seasonal, annual precipitation variation; while among tree species, the population density may exhibit sensitivity to environmental variation at larger time scales. A common feature shared by all species is that the central populations have a reduced sensitivity to environmental change due to their larger population size (cf. Carson 1956, Grant and Antonovics 1978). When environmental conditions change, the organism can avoid extinction either by adapting genetically to the new environmental conditions or by tracking its old environment across space (Pease *et al.* 1989). We argue that plants may tend to respond to environmental change by local adaptation while animals may tend to track their habitats through space.

Implications for biological conservation

The variations of population dynamics across a species' range are closely related to the dynamics of the species' range, i.e., expanding, contracting, or migrating. Such range dynamics could also be implied by the changes in patches within the species' range. Our models presented here can apply also to local scales, i.e., smaller habitat patches within the species' range. Our results show that dispersal and migration can maintain several separate populations in apparent demographic equilibrium. However, such equilibrium may be fragile due to the continuously changing environments. Central populations hold greater genetic diversity, whereas marginal populations are more sensitive to environmental changes. Because of the close linkage between populations within the species' range, conservation of both central and marginal populations is equally important (Brown 1984, Pulliam 1988, Lesica and Allendorf 1995, Furlow and Armijo-Prewitt 1995, Lomolino and Channell 1997).

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Figure legends

Fig. 1. A: Hypothetical Gaussian distribution and the relative levels of intra- and interspecific competition in central and marginal populations. The optimum environment, maximum habitat carrying capacity and population density are located at the center of the species' range (the vertical dashed line). B: Schematic illustration of the structure of the species' range assumed in the present model, in which the species' range was divided into a number of rings from the range center to the margin.

Fig. 2. Density-dependent and density-independent birth and death rates (b and d). The difference between b and d is emigration rate (e; when $b - d > 0$) and immigration rate (i; when $b - d < 0$).

Fig. 3. A comparison of migration rates from "source" to "sink" rings between less mobile species (mostly plants) and much mobile species (mostly animals).

Fig. 4. Spatial-temporal variation of migration over space within species' range and time (reproductive seasons). Immigration direction can be identified by the positive values near the species' range margin (sinks) and emigration is indicated by the negative values close to the range center (sources). Note that on the left of the figure, a larger "sink" is associated with a larger "source".

{{Fig. 5. In the conditions of without physical boundaries (e.g., the edge of mountain ranges or land-ocean boundaries), the deviation of the abundance curve of a species from typical Gaussian distribution may tell the direction of the species migration under environmental change. In this case, the species range is moving to the left where curve shows a much steeper slope than the right side.}}

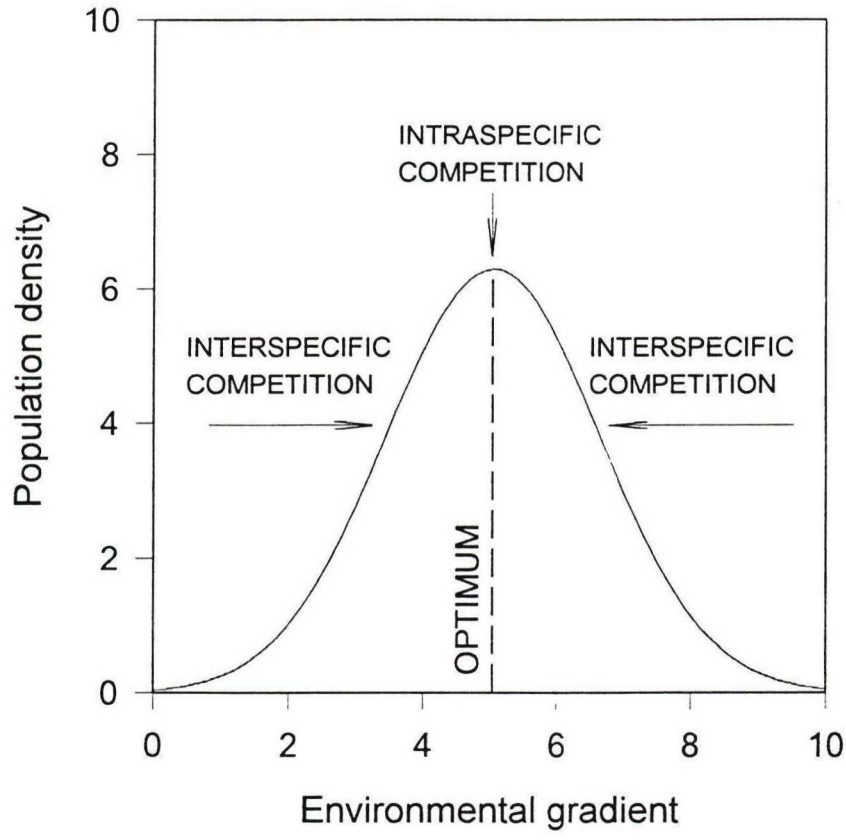
Fig. 6. Population dynamics across space from center to margin (rings) and time (reproductive seasons). {{Numbers indicate the relative population density (negative numbers are the emigrants and the positive numbers indicate the immigrants). The larger bottom patches closer to species' range center are identified as "sources" and the above smaller patches at the species range margin are identified as "sinks".}}

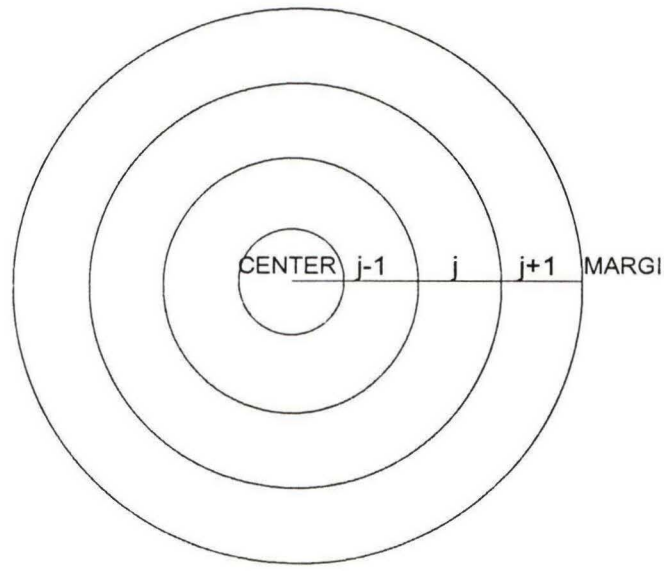
Fig. 7. Total population size in each ring (N_j) estimated based on Gaussian distribution of population density ($N_j = A_j n_j$; where A_j and n_j are the area and population density in jth ring, respectively).

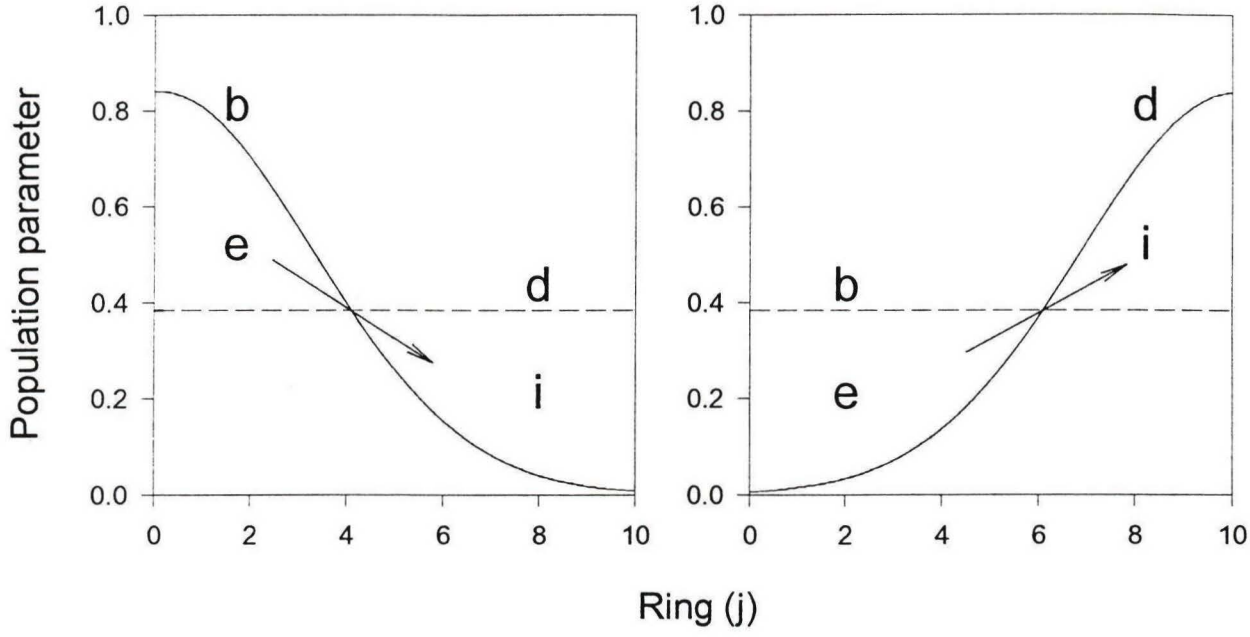
Fig. 8. Dynamic behavior of population in each ring across species' range. Note that the populations in central (ring 0), middle (ring 5), and marginal (ring 10) were shown here.

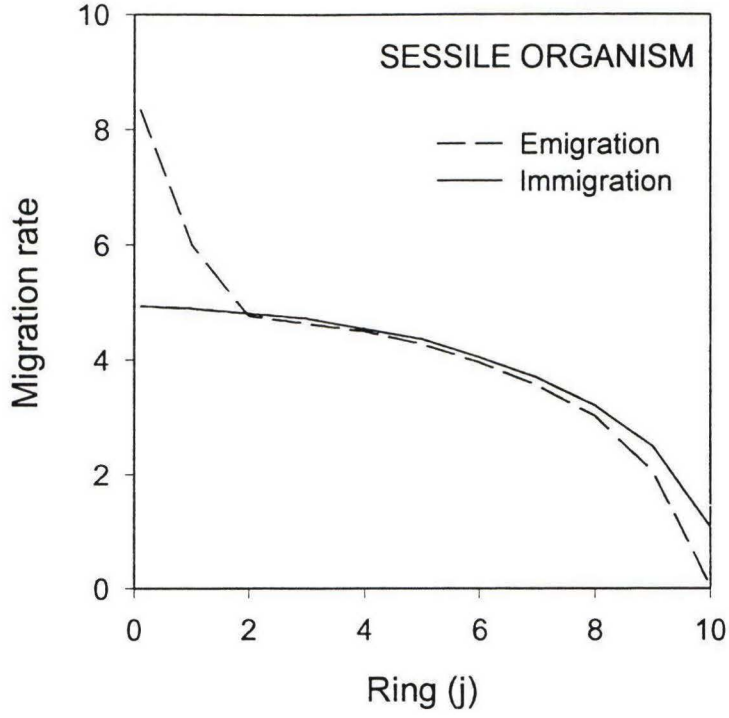
Fig. 9. Temporal variation in population density (measured by *CV* of population density over time) across species' range. {{Given the similar population sizes and time frames, plant species showed less sensitivities to stochastic environmental variation than animal

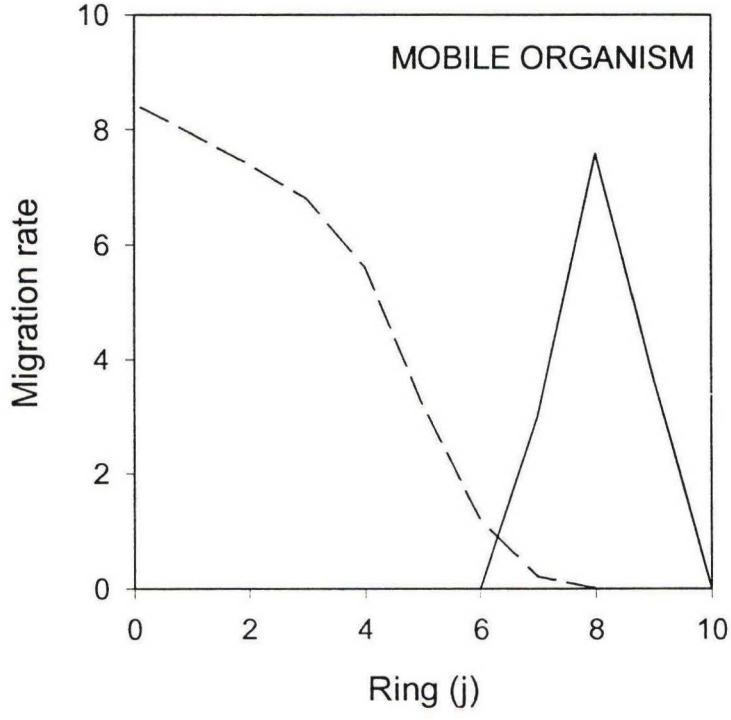
species. Note that *CVs* was measured using McArdle's $CV(\lambda)$ which takes proportional changes into account (for details, see McArdle 1995). }}

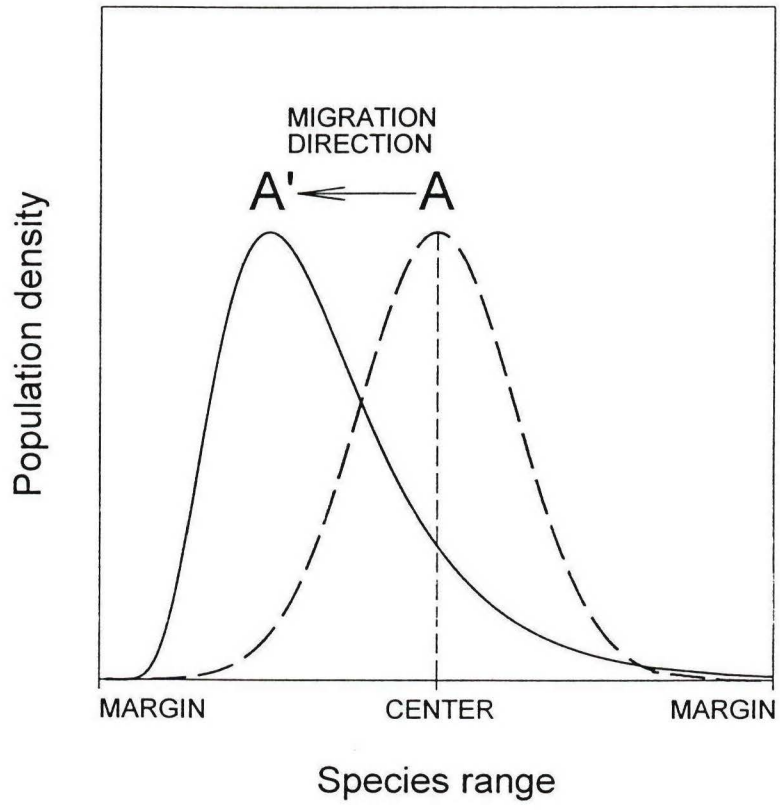

10
8
6
4
2
0
Population density
INTRASPECIFIC
COMPETITION
INTERSPECIFIC
COMPETITION
INTERSPECIFIC
COMPETITION
OPTIMUM
0
2
4
6
8
10
Environmental gradient

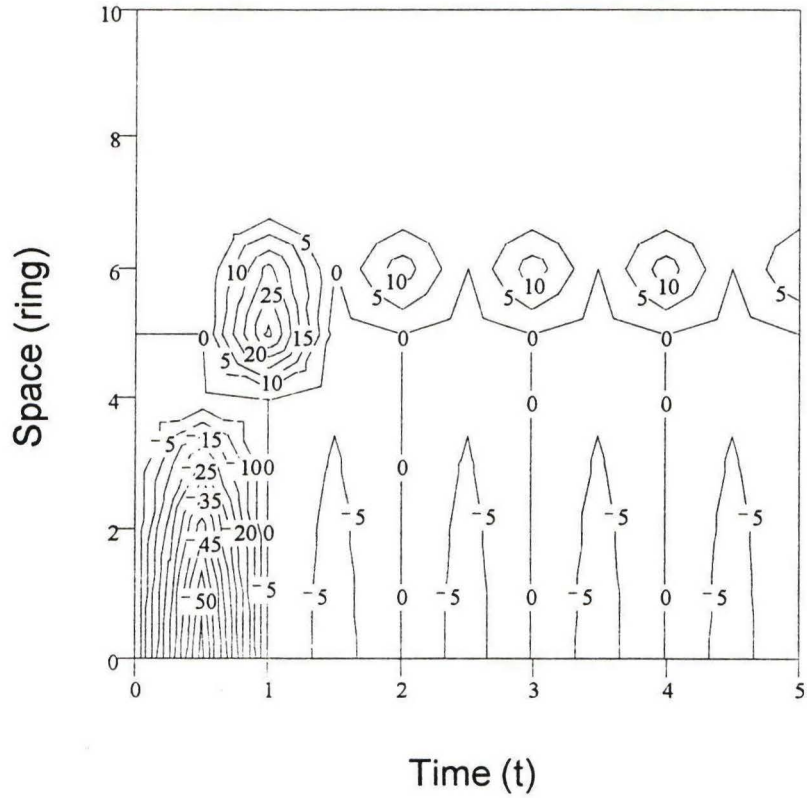

CENTER
j-1
j
j+1
MARGIN

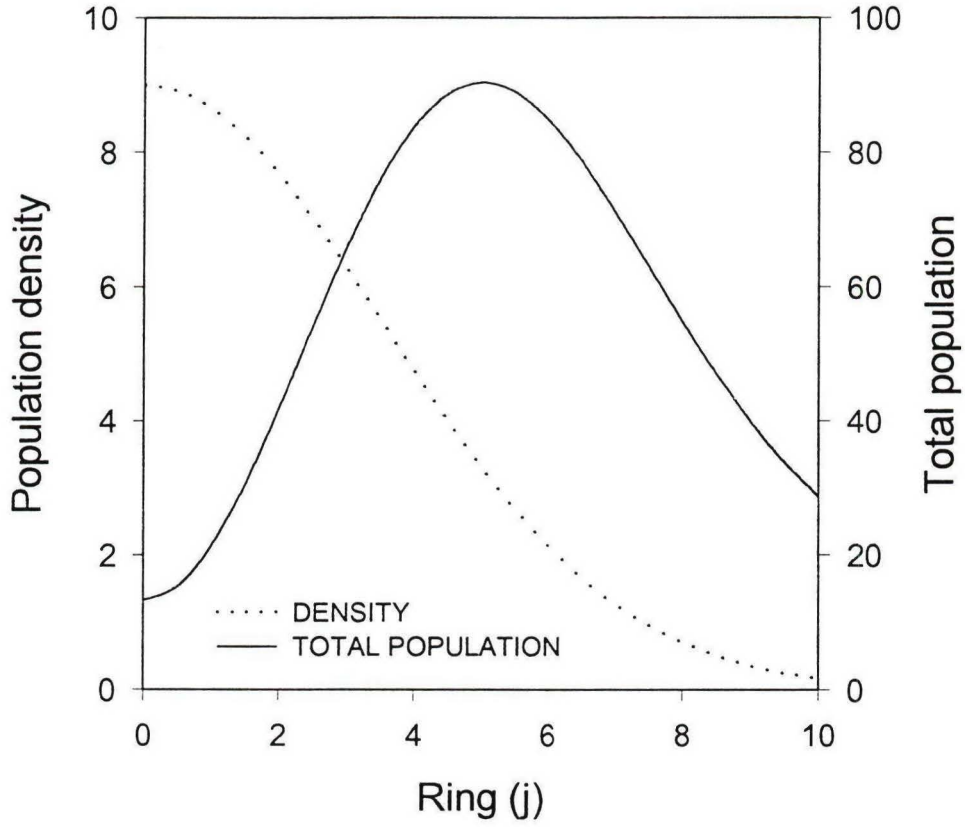

Population parameter
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
b
e
d
i
d
i
b
e
Ring (j)

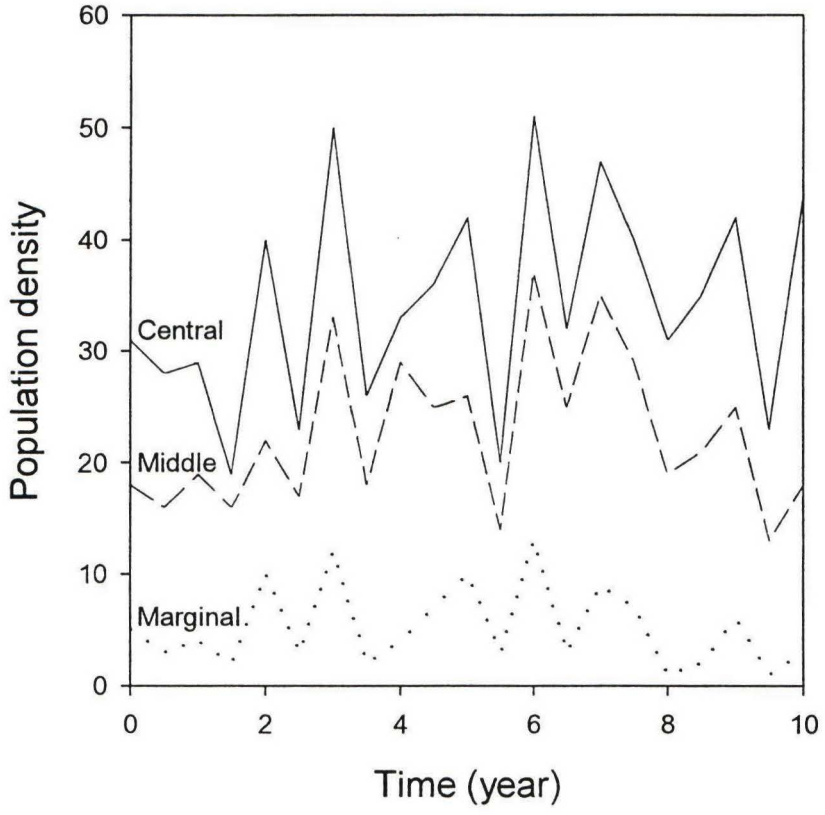

SESSILE ORGANISM
Emigration
Immigration
Migration rate
Ring (j)
0
2
4
6
8
10

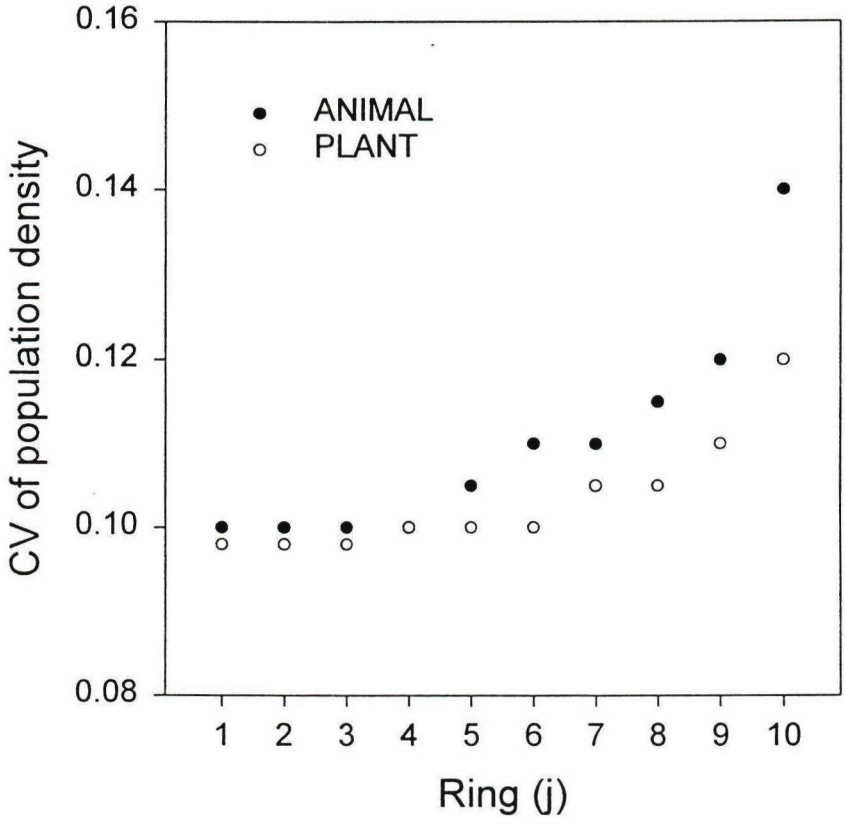

MOBILE ORGANISM
Migration rate
Ring (j)
0
2
4
6
8
10


MIGRATION
DIRECTION
A'
A
Population density
MARGIN
CENTER
MARGIN
Species range


Space (ring)
Time (t)
10
8
6
4
2
0
0
1
2
3
4
5
5
10
25
20
15
10
0
5
10
5
10
5
10
5
0
0
0


10
8
6
4
2
0
100
80
60
40
20
0
0
2
4
6
8
10
Population density
Total population
Ring (j)
DENSITY
TOTAL POPULATION


60
50
40
30
20
10
0
Population density
Central
Middle
Marginal
0
2
4
6
8
10
Time (year)


0.16
0.14
0.12
0.10
0.08
CV of population density
ANIMAL
PLANT
1
2
3
4
5
6
7
8
9
10
Ring (j)

SIMULATING LINEAR FOREST DYNAMICS IN GREAT PLAINS ECOSYSTEMS UNDER CHANGING CLIMATES

by

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ABSTRACT. Individually-based, spatially-explicit gap models that simulate the effects of environmental change on the forest growth and succession have been well-developed and broadly used. However, most of these models are not suitable for the highly fragmented linear forests in the agroecosystems where forests are a minor but ecologically important component of the landscape. In this study, we used SEEDSCAPE, a moderately modified gap model designed for cultivated landscapes of the Great Plains, to simulate the effects of global change on the dynamics of linear forests. We simulated the forest dynamics under different climatic scenarios using current climate data and general circulation models (GCM). We simulated the agroecosystem with both riparian zones and shelterbelts that had very different water regimes, different widths, and initial species richness. Results showed that warming climates reduced community biomass in the linear forests, especially in shelterbelts. Linear forests with higher initial planting species richness and smaller width produced higher biomass per unit area. This modified model presents the first example of using spatially explicit, individual-based forest gap models to the largely fragmented linear forest types in the region. The model showed promise in applications and will serve as the valuable starting point for modeling biological diversity and forest succession in human-dominated landscapes of the Great Plains under changing climates.

Key words: agroecosystems, global climate change, individual-based model, linear forest, SEEDSCAPE, simulation, succession, the Great Plains.

INTRODUCTION

Human-dominated agricultural ecosystems in the Great Plains may be especially sensitive to future climate change because of its flat and highly fragmented nature. In the Great Plains, woody areas, usually riparian zones and shelterbelts, comprise only a small portion of the agricultural landscape but they play important roles in crop production through their sheltering effects and in providing habitats or corridors for plants and wildlife in cultivated areas (Fig. 1a). The establishment and growth of the linear forests will influence crop production and plants and wildlife conservation. However, The growth and succession of these Great Plains forests have been largely overlooked and little information on temporal changes in community structure is available.

Individual-based, spatially explicit gap models that simulate the effects of climate change on the forest growth have been well-developed and broadly used (e.g., Botkin 1993, Liu and Ashton 1998). In these models, the establishment, growth, reproduction, and death of individual trees on a small plot of land (e.g., 10 x 10 m) are simulated, and in many studies, the forest dynamics are assumed to represent the surrounding forest. Since these models were designed for continuous upland forests, direct application to the highly fragmented linear forests in the Great Plains presents a number of problems.

For forested regions in which a single plot is assumed to represent a large area, gap models usually include ubiquitous seed dispersal (i.e., where the plot receives seeds of all species that might occur in the landscape). Establishment of trees is entirely dependent on the survival of seedlings rather than on their arrival on the plot. In reality, the location of any plot in the landscape will affect its probability of receiving seeds that disperse from other plots in the

landscape. Therefore, a single plot cannot be assumed to represent the entire forest accurately (Liu and Ashton 1998, Easterling et al. in press).

Linear forests result in a greater proportion of trees in the landscape that are on the forest's edge. Here they are likely to experience greater light availability and a different microclimate than interior trees. In addition, the Great Plains comprises a mixture of upland and riparian forests which experience very different water regimes. In upland areas in many parts of the Great Plains, the water table is extremely deep, and trees gain their water predominantly from precipitation. In riparian areas, water is also available from groundwater and adjacent streams or rivers. The availability of this water will fluctuate over time.

To accommodate the unique features of linear forest growth in agricultural landscapes, we developed a new model, SEEDSCAPE (Guertin et al. 1997). Based on existing gap models, this model was constructed to overcome the limitations of existing forest models, and to provide a starting point for understanding ecological processes in these heavily human-dominated landscapes. One important question is what are the ecological implications of future climate change and varying the dimensions of these linear forest corridors. Warming climates are likely to change the existing forest structure and dynamics and the linear forests with different widths may support different biodiversity values and crop productions.

In this paper, we use SEEDSCAPE to simulate the dynamics of riparian zones and shelterbelts with different species richness and widths and under different climatic scenarios. The goal is to develop design criteria for woody corridors' establishment and management in terms of their ideal size (length and width), spatial arrangement, and optimal density that can better balance crop production and biological conservation. We ask the following questions: (1)

How will global climate change affect the growth of linear forests in the Great Plains? (2) How does forest width affect community biomass and evenness? (3) How does planting species richness affect the forest growth under different climatic scenarios?

THE *SEEDSCAPE* MODEL

The SEEDSCAPE model is derived from a gap model, JABOWA II (Botkin 1993). It simulates forest dynamics by monitoring the growth of individual trees as a physiological response to competition, temperature and CO_2 concentration and the availability of light, nutrients, and water under a changing climatic scenario in a spatially explicit landscape. The main features of the present SEEDSCAPE model include:

(1) Extension of the single-plot approach to an entire landscape of multiple plots (10 x 10 m^2) over a 100 x 100 grid (1 km^2; Fig. 1b). This can incorporate the fundamental differences between forest stands with small edge-to-area ratios (e.g., large forested tracts) and ones with large edge-to-area ratios (e.g., riparian forests). In addition, because the 1 km^2 landscape is not a closed system, plots along the edges of the landscape can be designated as seed sources. These plots contain species that are found outside the 1 km^2 landscape, but are close enough to deliver seeds to the landscape. Within this landscape, each plot is assigned particular values for soil type, initial vegetation, and whether the plot is in a riparian or upland location. The soil type determines moisture capacity, available nitrogen in the soil, soil depth and the depth to the water table. Initial vegetation determines whether the plot is cultivated and therefore incapable of supporting trees, or wooded. The species and diameter of all trees on each wooded plot are assigned at the start of the model run.

(2) Allowing seed dispersal among all plots in the simulated landscape (each species can have up to three dispersal mechanisms within a total of eight dispersal categories) linking the entire array of species that occur in a given area and connecting all simulated plots. SEEDSCAPE uses the dispersal algorithm from the SEEDFLO model (Hanson et al. 1990). In this algorithm each plot is used as a potential seed source if it contains trees large enough to produce seed and if those trees actually produce seeds in a given year as determined by the species-specific probability of seed production. Initially each tree's age is set to the minimum age for seed production unless explicitly set to another age. For each tree on each plot, the probability of seeds reaching each of the other potentially wooded plots in the landscape is determined by the simple distance-decay function, $P_{ij} = d_j^{-\varphi}i$, where i is a species-specific dispersal agent, P_{ij} is the probability of a seed dispersing to plot j given a dispersal agent i, d_j is the distance in meters to plot j, and φ_i is the dispersal parameter for a dispersal agent i (Okubo and Levin 1989). Once seeds have arrived on a plot, the seedling establishment, growth, and mortality are similar to other existing gap models. The specific equations in SEEDSCAPE are the same as those in JABOWA-II (Botkin 1993).

(3) Locally variable water tables: For upland plots, the availability of water is the same as in JABOWA-II, and is determined by precipitation and by the water table. Because the water table in our study areas is extremely deep in upland locations, it is not normally a factor in tree growth. In riparian plots, however, the soil may be completely saturated due to a shallow water table resulting from flooding along water courses following precipitation events. SEEDSCAPE therefore allows for variable local water tables in riparian plots. The water table varies with water volume in the streams, which is in turn a function of runoff from surrounding agricultural

fields. SEEDSCAPE uses the curve number method developed by the USDA-Natural Resources and Conservation Services (USDA-NRCS 1972) to calculate runoff volume following precipitation events.

STUDY SITE AND FIELD DATA

Field study was conducted in the forest corridors about 20 m wide at Mead, Nebraska which are typical of those found in the eastern and central Great Plains. The focal 1 km^2 landscape includes riparian zones along a drainage slough, planted shelterbelts, and crop fields. The southern half of the forest corridors within the landscape was cleared in 1971 and the northern half was cleared in 1979. Totally 25 tree and shrub species were found in the study area. Field data were collected from existing vegetation in 1995 from five 10 x 10 m plots along the corridor length. None of the survey plots contained all 25 species found at the study site. The number of stems of each tree species and diameter (DBH) of all trees were recorded, and a visual survey was made of the surrounding area to estimate the number and diameter of the potential seed source trees there. Twelve species were in the 1 km^2 landscape including the seed source plots and 10 of these species were found in the riparian strip. The forest corridors were initialized to have no woody vegetation at the start of the simulations.

Five iterations of a 400-year simulation for both shelterbelts and riparian zones with three different corridor widths (10, 20, and 30 m) were simulated under both current climatic conditions and RegCM2 climatic change scenarios. RegCM2 is a regional climate model developed by National Center for Atmospheric Research (NCAR; for details, see Giorgi et al. 1993a, b). Monthly weather data were obtained for 1967-1995 from the nearest weather station

near Mead, Nebraska. Soil types were determined from Saunders County soil survey maps.

We made cross-comparisons in total biomass and community evenness between: (1) current climatic conditions and global warming scenarios; (2) three corridor widths (10, 20, 30 m with total planted areas kept the same); (3) a species rich community (10 spp.) and less a diverse community (4 spp.). Finally, we simulated the population dynamics of each individual species under these different conditions.

SIMULATION RESULTS

It took 70-80 simulation years for both riparian zones and shelterbelts to reach a steady state under both current climatic conditions and climatic warming. After that biomass and species composition kept relatively constant over the other 320 simulation years.

Effects of climatic warming:

Given a certain level of species richness or width, the linear forests produced significantly lower biomass under warming climatic scenarios than under current climatic conditions (Figs. 2, 3, 4). This was especially remarkable in planted shelterbelts (data not shown). There was no evidence that climatic warming would cause greater spatial variation in biomass among simulated plots (Figs. 2, 3) but climatic warming did cause greater variation in biomass (or higher dominance) among component species (Fig. 5 vs. Fig. 6).

Effects of species richness

Linear forests with lower species richness (4 spp. vs 10 spp.) produced less biomass but

resulted in higher spatial variation in biomass among simulated plots (Fig. 4; Fig. 2 vs. Fig. 3). However, there was no clear evidence that higher species richness could lead to lower spatial (among simulated plots) and temporal (among simulated years) variation in community biomass. The linear forests with higher species did produce higher biomass and higher community evenness under both current and warming climates (ANOVA, $P < 0.01$).

Effects of corridor width

Given the total forested area (many narrower corridors or fewer wider ones), significant effects of linear forest width on total biomass were detected (paired t-test, $P < 0.05$) but the spatial variation in biomass across simulated plots was smaller in wider corridors than in narrower corridors (t-test on standard deviation of biomass among plots; $P < 0.05$). We did not see any clear evidence that corridor width affected community evenness (paired t-test, $P > 0.05$). Forest width did not have any significant effects on the performance of individual species. Although the trajectories of each species were somehow different in narrower (10 m) and wider corridors (20 m), there were no significant differences in the relative importance of each species measured by biomass (data not shown).

The forests with higher species richness (10 species) showed great differences in biomass among the forests with different widths than those with only four species (Fig. Xx).

Another notable change was the difference in the switches of species dominance when the forests were designed with different widths, even though the forest species composition was still the same. For example, ... (Data not shown).

Responses of individual species

Among the 10 species (Table 1) used in our simulation for riparian zones under both current climate conditions and warming trends, *Prunus americana* showed a dramatic decline, especially under warming climate. Following the decline of *Prunus americana*, *Acer negundo* and *Morus alba* showed similar trends with the former dominating in the first 130 simulation years. After that period, both species declined with *M. alba* almost totally eliminated from the local community, but *Fraxinus pennsylvanica* then became the most dominant species, followed by *A. negundo* and *Populus deltoides* (Fig. 5).

In the shelterbelt with four species only, the patterns were different. *P. americana* and *M. alba* exhibited similar patterns as in riparian zones. But *A. negundo* became the dominant species after the first 10 simulation years and then continued its dominance, with its biomass keeping relatively constant over time. Under normal climatic conditions, *P. americana* and *M. alba* still kept their minimum existence over time, however, under warming climates, both species were eliminated from the local community after 20 and 150 years, respectively (Fig. 6).

DISCUSSION

The modified model, SEEDSCAPE, presents the first example of using spatially explicit, individual-based forest gap models to simulate successional processes in the largely fragmented linear forest types (riparian zones and shelterbelts) of the Great Plains. Although our results are still preliminary, the outcomes from our simulations suggest that the model performs reasonably well. It successfully detected the potential effects of global climate change on biomass and community evenness in both riparian zones and shelterbelts. The model also successfully

revealed the switches in species dominance under different climatic scenarios over time and the highly individualistic responses of the different species.

The application of SEEDSCAPE is to test the effects of climate change and forest corridor widths on the growth of component species in order to better select species and arrangements of these forest types in agroecosystems of the Great Plains. In this study, there is no evidence that wider corridors support higher plant community evenness. One reason could be that the model does not simulate all species that can potentially occur in these systems, which is still one of the weakness of the current SEEDSCAPE model (see below). The small differences in importance values between the smaller corridor widths (10, 20, 30 m) suggest that light penetration into the interior of the corridor does vary significantly at these widths.

Using different GCM models to examine the effects of global climate change would certainly produce different results. Using the regional climate model, RegCM2 (see Giorgi et al. 1993), our simulation results indicate that lower biomass and community evenness would be produced regardless of the original species richness and forest shape (i.e., width). However, it is not yet clear at this time from our model structure why spatial variation (standard deviation) in biomass across simulated plots became greater after 225 simulation years in the linear forests with 10 species under both current climate and warming climate (Fig. 2).

Our simulation results support results from earlier studies that demonstrated a richer community would produce higher biomass and community evenness. However, there was no clear relationship between species richness and community stability (measured as *CV*s on biomass over time) in our simulation results.

Based on the assumptions and procedures used in this research, the results suggest that

simulated changes in the forest corridor width of Great Plains do have a significant effect on successional characteristics of those forests until the widths become quite large. We infer from these results that a trend toward protection of these forest strips leading to the growth of forest widths to much greater than 20m???? may have significant effects on community structure.

There are some weaknesses in the SEEDSCAPE model: (1) Feedbacks between trees and environment have not yet been incorporated into the model (forest growth itself will modify the local and regional environments; see Chen et al. 1999); (2) Under-story species are not yet considered. The present model only includes trees and dominant shrubs. This is a result of two factors: First, too expensive in terms of computing (time and space), and second, not enough empirical data are available. Ideally all component species in different plant life forms (i.e., shrubs and herb species) should be included in future modeling improvement. This would require a design of smaller patches for shrubs and herbaceous plants nested within the original large patches for trees.

Wooded corridors are expected to expand throughout much of the Great Plains because of planting, suppression of wildfire (Knight et al. 1994), and reduced river flows in some riparian areas (Johnson 1994). Future revisions of the model focusing on the expansions of forests over time, dispersal abilities, and the spatial configurations of riparian zones and shelterbelts across the agricultural landscape to the regional level are critically needed.

In summary, SEEDSCAPE model provides a feasible method for increasing our understanding of forest succession in Great Plains agroecosystems. Our simulation results showed that the structure and dynamics in the linear forests (riparian zones and shelterbelts) were significantly different under different climatic conditions. Forest design (i.e., planting

species richness and width) and management practices can significantly affect future forest structure and dynamics. This modified model presents a good example of using spatially explicit, individual-based forest gap models to the largely fragmented linear forest types in the region. It shows promise in various applications and will serve as a valuable starting point for modeling biological diversity and forest succession in human-dominated landscapes of the Great Plains.

ACKNOWLEDGMENTS

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Table 1. Species-specific reproductive parameters and dispersal agents. SAP is the max. # saplings added per year. Age_{min} and Age_{max} are the minimum and maximum ages at which a tree can produce seeds. $Pr_{(seeds)}$ is the probability that a tree will produce seeds in a given year. Dispersal agents are based on Malanson and Armstrong (1996).

Species	SAP	Age_{min}	Age_{max}	$Pr_{(seeds)}$	Dispersal agent	
					Primary	Secondary
Acer negundo	3	30	100	1.0	1	
Celtis occidentalis	3	35	200	0.8	5	7
Fraxinus pennsylvanica	10	15	150	0.8	2	8
Juniperus virginiana	3	10	150	0.8	6	
Morus alba	3	5	125	1.0	6	
Populus deltoides	10	25	150	0.9	4	7
Prunus americana	60	10	40	1.0	5	7
Salix amygdaloides	10	10	85	0.9	4	
Ulmus pumila	15	15	70	0.5	2	
Ulmus rubra	3	15	200	0.5	2	

Table 2. Values of φ for each dispersal agent used in dispersal equation. Dispersal agents are based on Malanson and Armstrong, 1996.

Dispersal agent	i	φ
Wind (short distance)	1	1.07
Wind (intermediate)	2	1.04
Wind (intermediate)	3	1.01
Wind (long-distance)	4	0.90
Mammal	5	1.02
Bird (blue jay)	6	0.94
Bird (other)	7	0.99
Gravity	8	10000.00

FIGURE LEGENDS

Figure 1. The three major spatial components (riparian zones, shelterbelts, and crop lands) in the agricultural landscapes of the Great Plains (photo provided by G. Wells. Below: A fraction of the spatially explicit agricultural landscape (1 km^2) simulated using SEEDSCAPE which contains 10,000 10 m x 10 m plots (Black: riparian zone, shade: shelterbelt, open: crop lands).

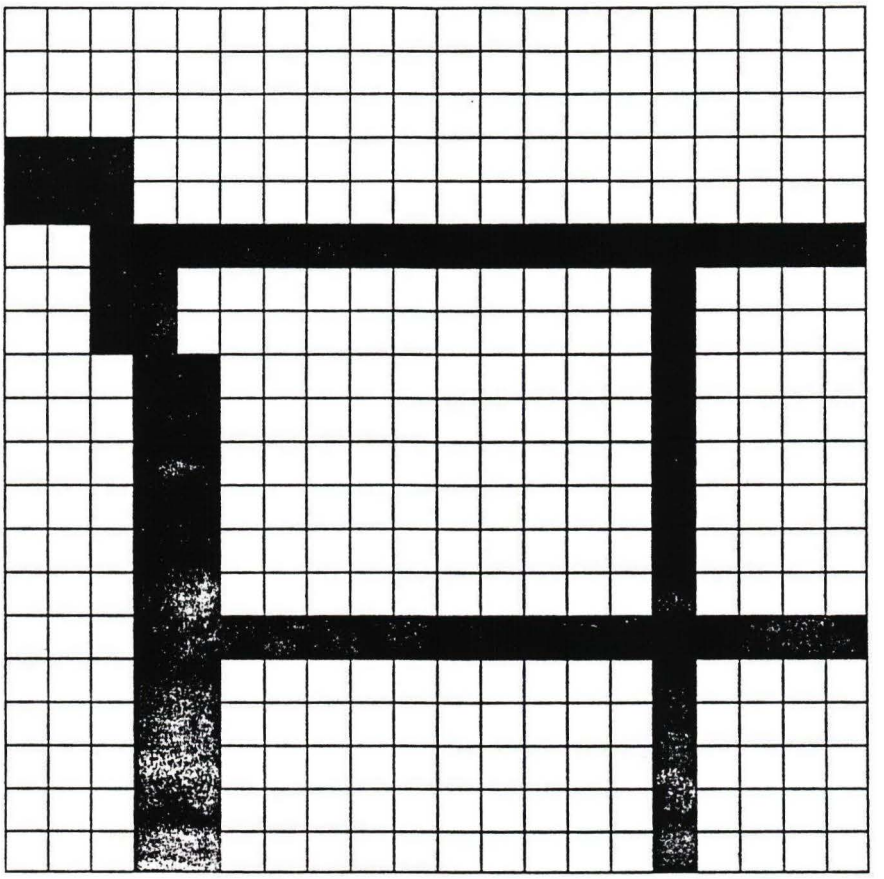
Figure 2. Temporal variation in biomass (vertical bars indicate the spatial variation of biomass among simulated plots) in the simulated forests with 10 species under both current and warming climates.

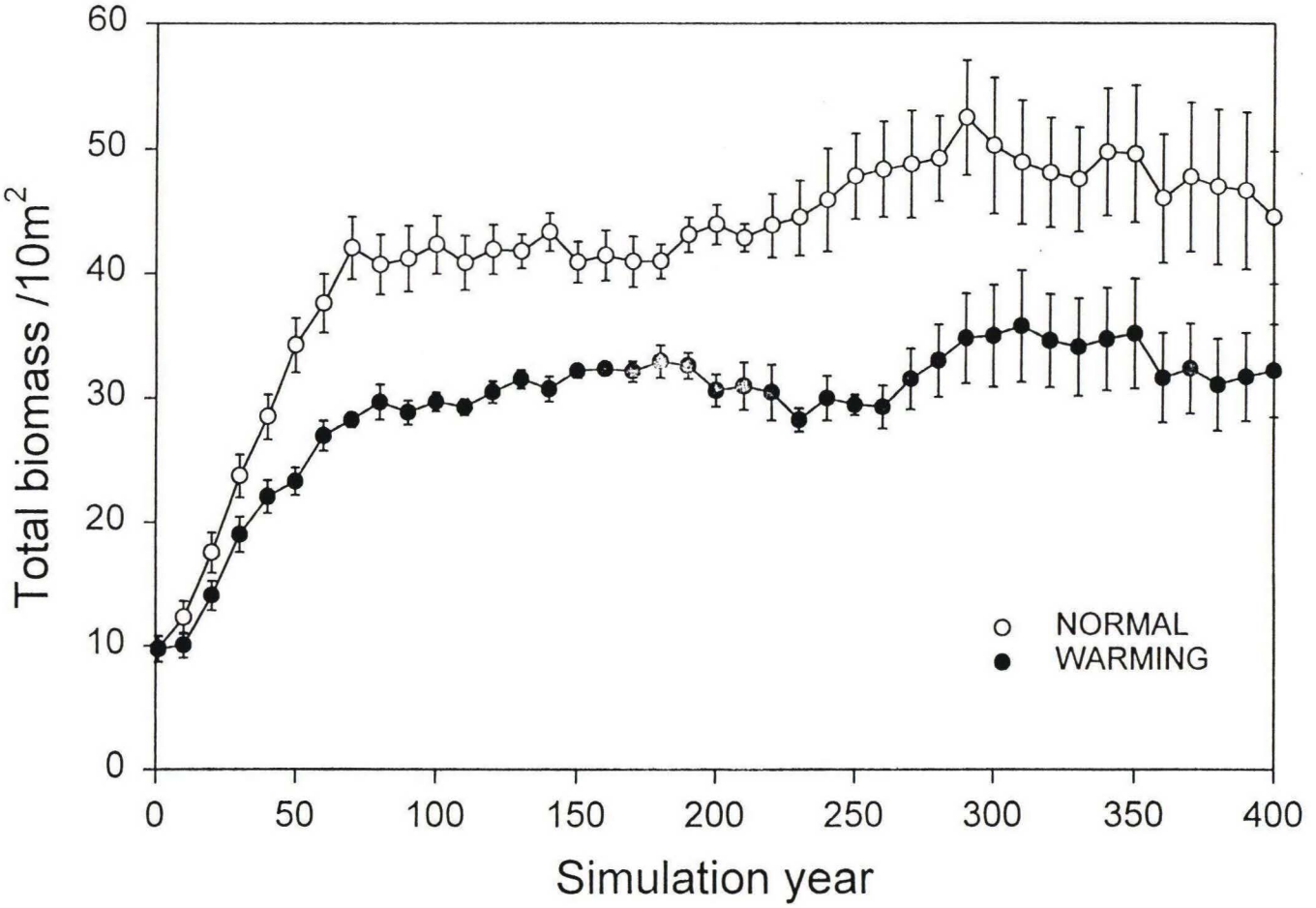
Figure 3. Temporal variation in biomass (vertical bars indicate the spatial variation of biomass among simulated plots) in the simulated forests with four species under both current and warming climates.

Figure 4. Comparison of temporal variation in biomass in the simulated linear forests with 10 and four species under both current climatic conditions and climatic warming.

Figure 5. Temporal variation in biomass of individual species in the simulated forests with 10 species under current and warming climates.

Figure 6. Temporal variation in biomass of individual species in the simulated forests with four species under current and warming climates.




Total biomass /10m^2
Simulation year
NORMAL
WARMING
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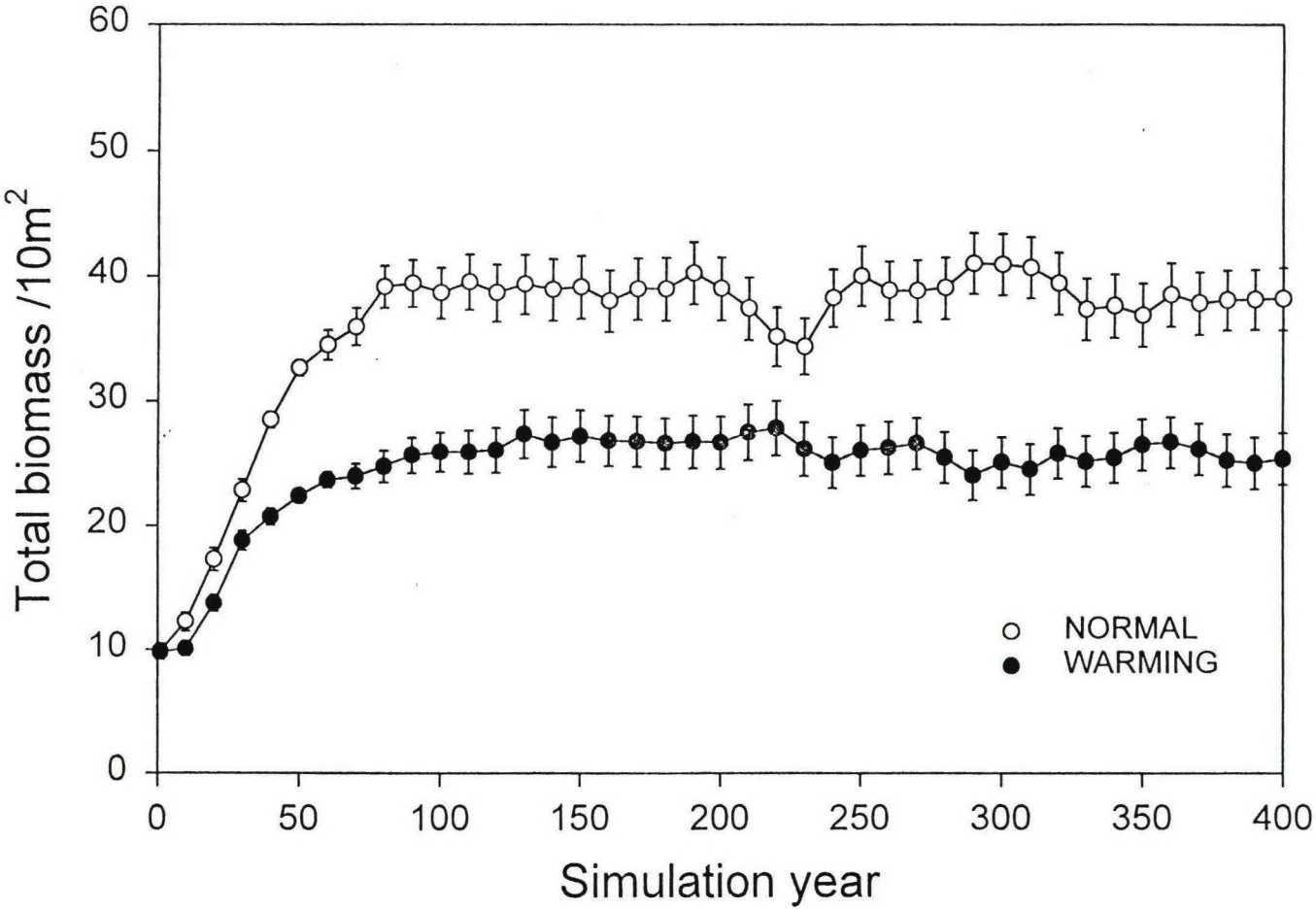
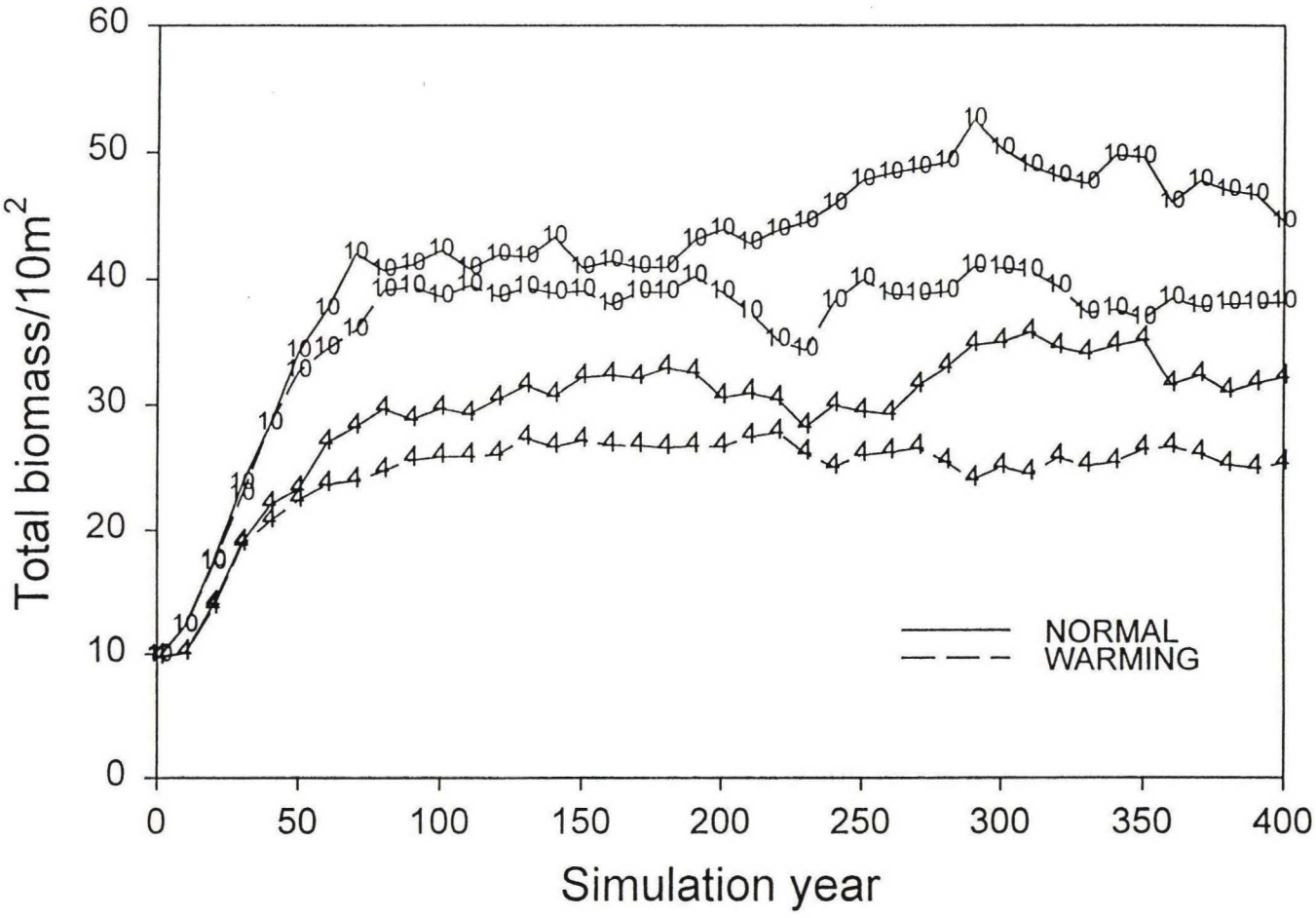
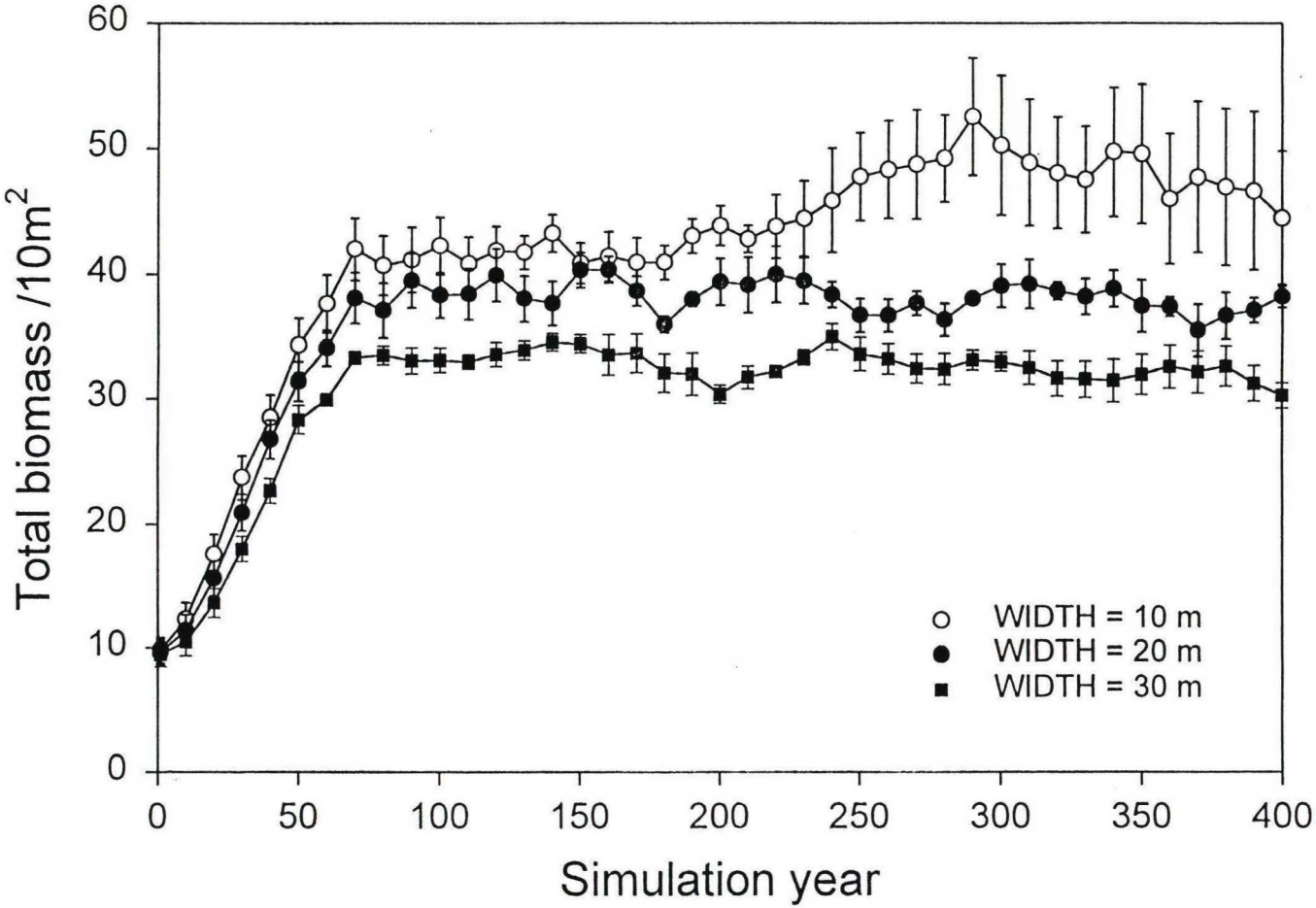
10
20
30
40
50
60
0
50
100
150
200
250
300
350
400


Total biomass /10m2
60
50
40
30
20
10
0
0
50
100
150
200
250
300
350
400
Simulation year
NORMAL
WARMING


Total biomass/10m^2
60
50
40
30
20
10
0
0
50
100
150
200
250
300
350
400
Simulation year
NORMAL
WARMING


Total biomass /10m^2
Simulation year
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10
20
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40
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60
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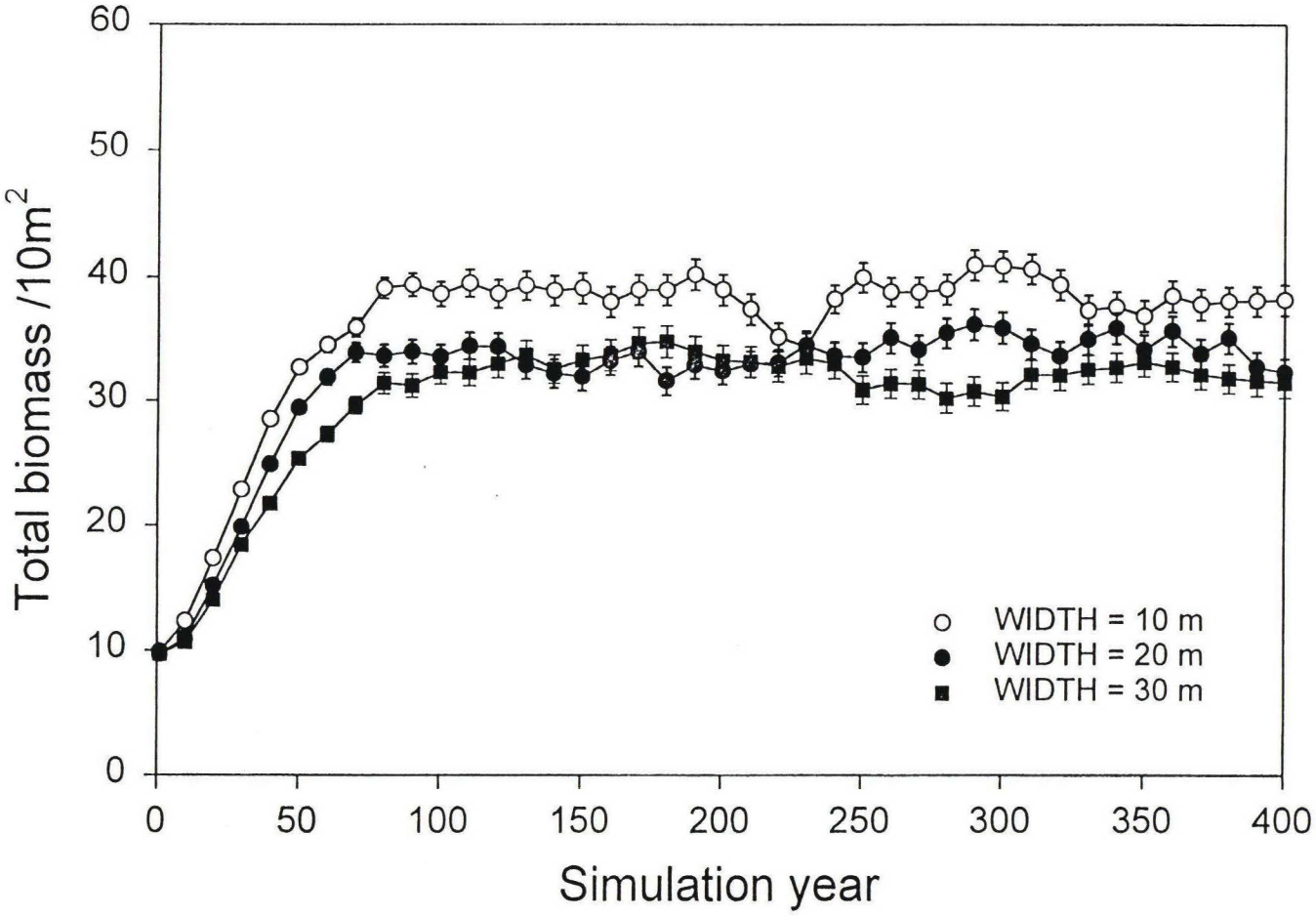
50
100
150
200
250
300
350
400


Total biomass /10m^2
Simulation year
0
10
20
30
40
50
60
0
50
100
150
200
250
300
350
400
WIDTH = 10 m
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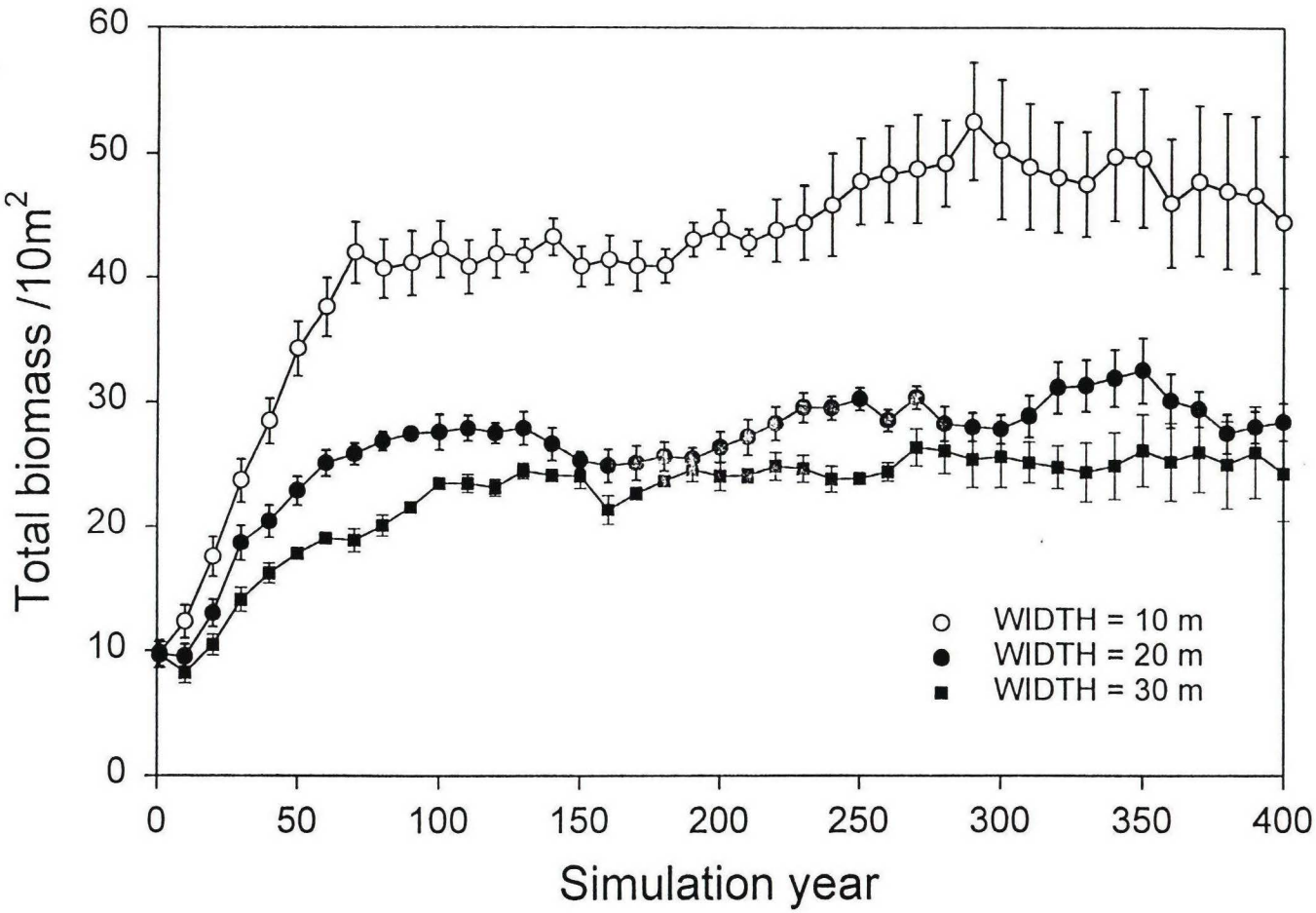
WIDTH = 30 m


Total biomass /10m2
Simulation year
WIDTH = 10 m
WIDTH = 20 m
WIDTH = 30 m
0
10
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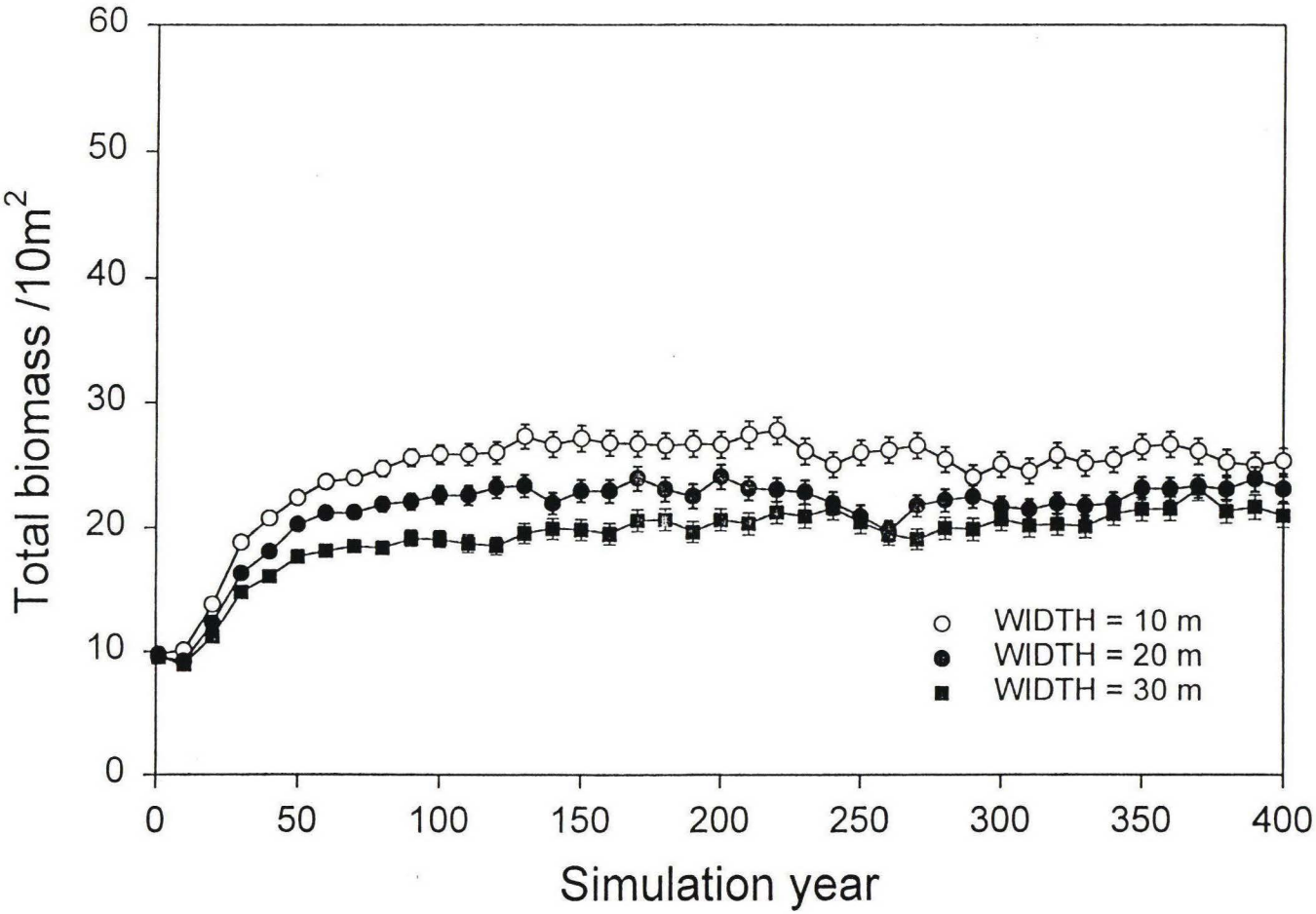
Total biomass /10m2
60
50
40
30
20
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0
0
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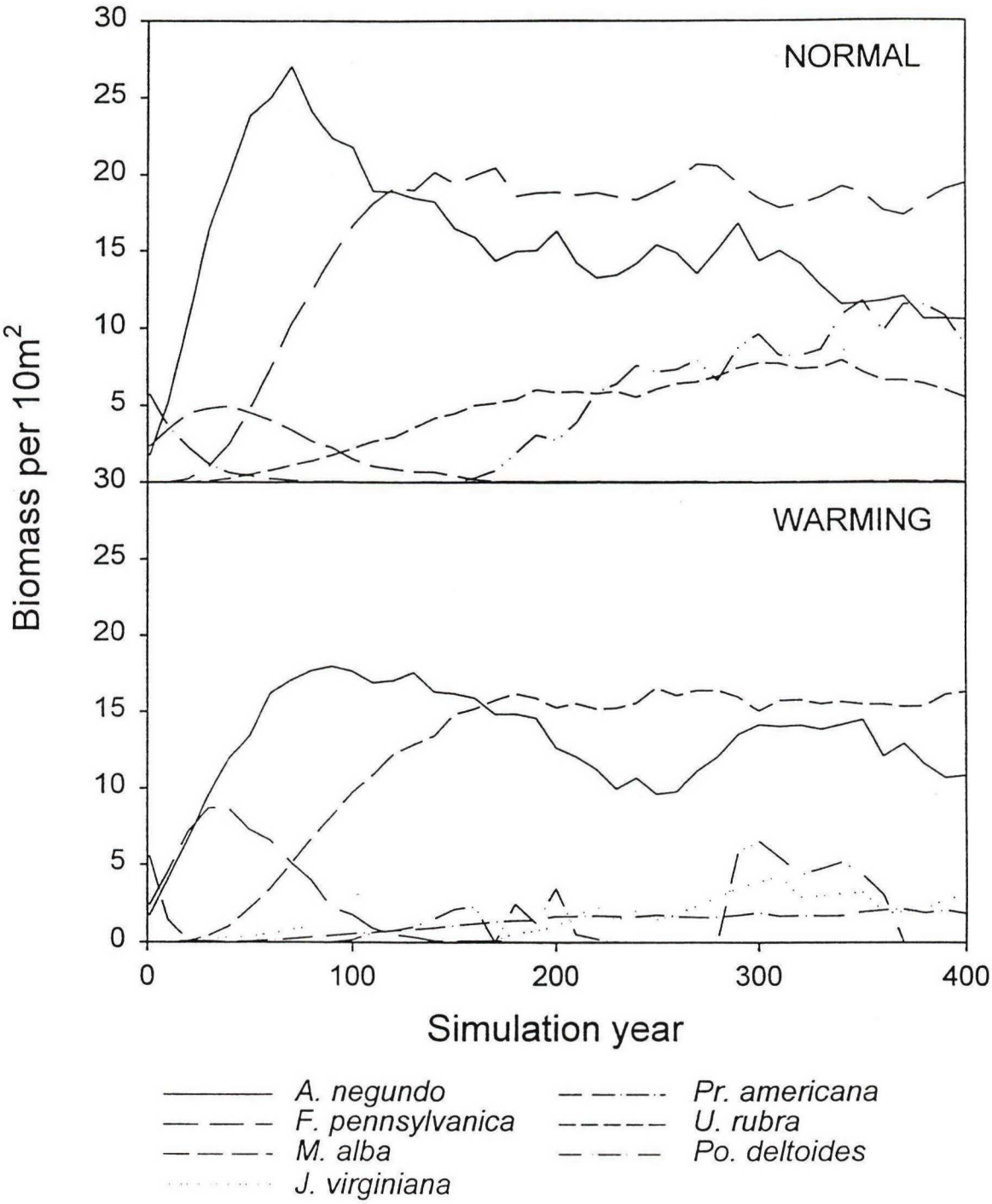
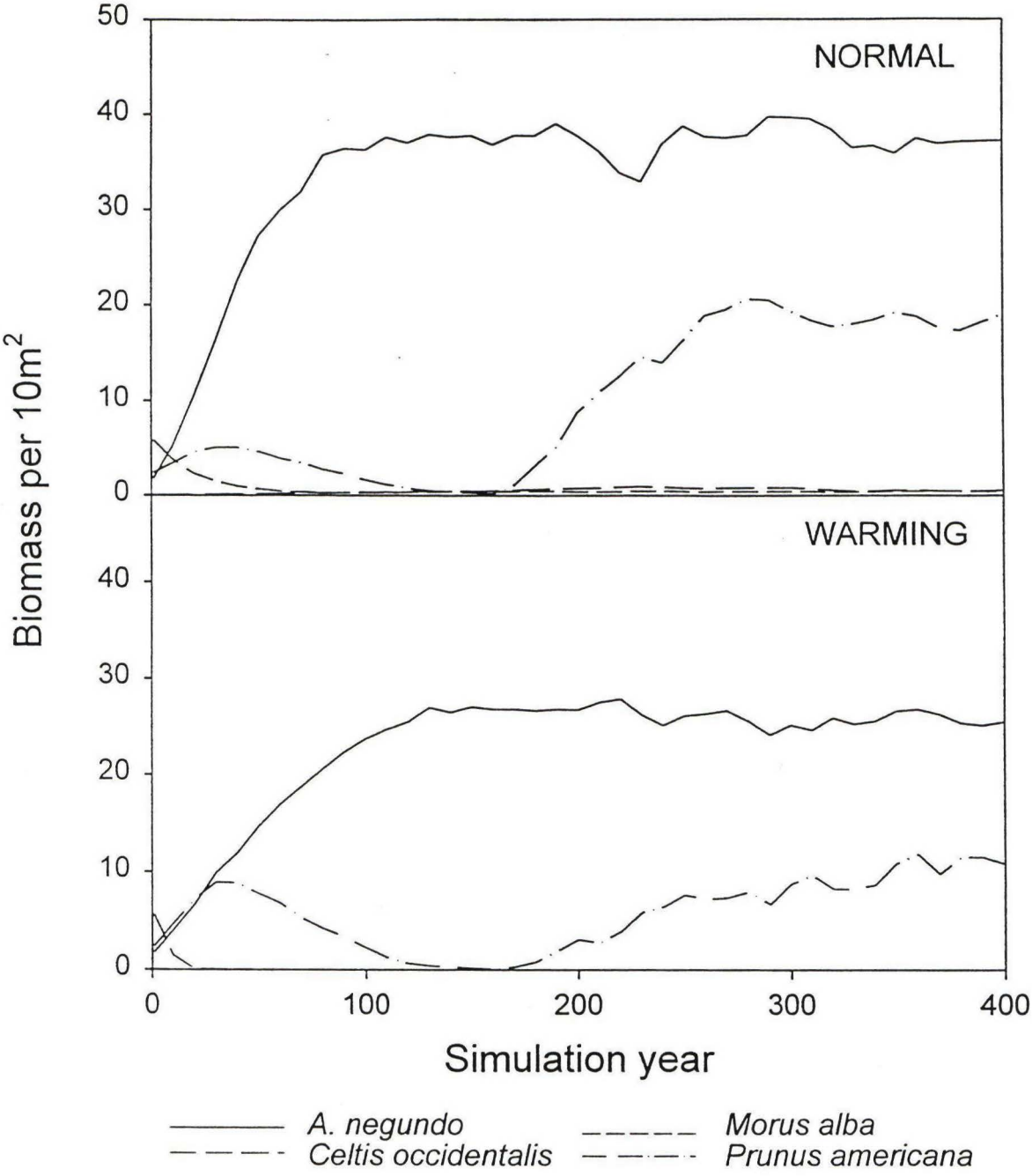
350
400
Simulation year
WIDTH = 10 m
WIDTH = 20 m
WIDTH = 30 m


NORMAL
WARMING
Biomass per 10m2
Simulation year
0
100
200
300
400
5
10
15
20
25
30
A. negundo
F. pennsylvanica
M. alba
J. virginiana
Pr. americana
U. rubra
Po. deltoides


NORMAL
WARMING
Biomass per 10m2
Simulation year
0
10
20
30
40
50
0
100
200
300
400
A. negundo
Celtis occidentalis
Morus alba
Prunus americana